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Abstracts

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INVITED PERCEPTION LECTURE

◆ Perception and application: the relation between fundamental research and applied engineering

T J B Swanenburg (Multimedia Technology, Philips Corporate Research,
Prof. Holstlaan 4, 5656 AA Eindhoven, The Netherlands)

In recent years a large number of technical breakthroughs have enabled creation, storage, distribution, and display of practically unlimited amounts of information via systems of increasing complexity. The results of these technical achievements have become evident in the digitisation of consumer electronics, in mobile communications, in car electronics, in personal computers, and in many other applications. The simple fact that, in principle, mankind has reached the stage where technically speaking 'everything is possible' creates the need for a new paradigm in directing fundamental research. Although the need for a real understanding of observed phenomena is at least equally strong as in the past, such understanding is no longer sufficient in directing further investigations. In many cases a direct interaction with applications is necessary to reduce the number of options in a meaningful way, and to make measurable and reproducible progress in fundamental research.

INVITED LECTURE: EARLY VISUAL PROCESSING

◆ Neural mechanisms for the analysis of contrast in normal vision and during saccadic eye movements

D C Burr (Istituto di Neurofisiologia del CNR, Via S Zeno 51, 56100 Pisa, Italy)

Over the last thirty years, many psychophysical techniques have been applied successfully to study the neural mechanisms responsible for coding image contrast. Some selected studies are reviewed to show how a variety of adaptation, masking, and summation techniques have elucidated the spatial and temporal properties of early visual mechanisms.

We have recently applied some of these techniques to study vision during saccadic eye movements. The results suggest that sensitivity to luminance-modulated gratings of low spatial frequency is greatly reduced during saccades (by up to 1 log unit), but that to high-spatial-frequency gratings and to equiluminant gratings of all spatial frequencies is not reduced during saccades, but in many cases was actually increased. Measurements of contrast sensitivity during forward, backward, and simultaneous masking (designed so that either the test, or the mask, or both could occur during saccades) suggest that the inhibition occurs before the site of masking (possibly as early as the lateral geniculate nucleus). The selective decrease in sensitivity of low-frequency luminance gratings together with the unchanged (or enhanced) sensitivity to equiluminant gratings suggest that the inhibition is confined to the magno pathway. This could dull the otherwise disturbing sense of fast low-spatial-frequency image motion, while the normal (or possibly enhanced) activity of the parvo pathway could supply the continuity of vision to bridge saccades.

EARLY VISUAL PROCESSING I

◆ Is the jazz in Op Art central or peripheral?

R L Gregory (Department of Psychology, University of Bristol, Bristol BS8 1TN, UK)

Closely spaced high-contrast lines, such as the Mackay Rays and Bridget Riley Op Art pictures, produce a marked visual disturbance—jazzing. Mackay [1957 *Nature (London)* **180** 849–850] attributed this to some kind of neurally central saturation due to the information redundancy of his radiating-rays figure. Recently, Zeki et al (1993 *Proceedings of the Royal Society of London, Series B* **252** 215–222) have reported brain-scan experiments indicating similar cortical activity for such illusory and real movement. But there might, however, be a physical peripheral motion input, accounting for jazzing of repeated high-contrast contours. It is well known that the lenses of the eyes are continually hunting for accommodation, for best focus. As the sign of the error is not available, hunting is an essential feature of the accommodation system. It produces small changes of image size, and possibly some sideways motion, peaking at around 0.5 Hz.

I find the jazzing is greatly reduced, or entirely disappears, when these figures are viewed through a pinhole. The pinhole increases the depth of field—essentially turning the eye into a pinhole camera—so the hunting of the lens now has only second-order effects. Eye movements are not affected. It remains to try adding optical oscillating changes of size, with small axial shifts, while retaining the pinhole, presumably to restore the lost jazz to MacKay's figure and to punctured Op Art.

◆ **Higher-level edge detectors mediate complex orientation discriminations**

L A Olzak, T D Wickens, J P Thomas (Psychology Department, University of California at Los Angeles, Los Angeles, CA 90024-1563, USA)

Many computational models of spatial vision posit higher-order mechanisms that signal spatially complex stimulus features, such as lines, edges, or textural information. In previous work we have described a model of how edge and texture mechanisms could be constructed to account for suprathreshold discrimination performance. We have recently developed a concurrent-response discrimination paradigm and related analyses that allow us to reconstruct empirically properties of mechanisms mediating judgments about complex stimuli. Our techniques allow us to evaluate the degree to which two very different components of a complex stimulus are processed independently. When nonindependence is found, we are able to assess separately the effects of direct sensory interaction (excitation or inhibition), correlated noise, and attention. We have obtained results for the mechanisms underlying orientation and spatial-frequency judgments for edgeline stimuli. Test stimuli are sets of four complex gratings composed of the sum of a vertical low-frequency (near 3 cycles deg^{-1}) and high-frequency (near 15 cycles deg^{-1}) component. Observers make two two-alternative discrimination judgments, one based upon the low-frequency component, the other based on the high-frequency component. When the judgments are based upon small differences in spatial frequency, the components are processed independently with uncorrelated noise. However, we confirm our previous report (obtained with 3 cycles deg^{-1} + 15 cycles deg^{-1} plaid stimuli) that observers cannot simultaneously attend to the different spatial scales. On the other hand, when the task is based upon tiny differences in the orientation of the components, observers cannot make independent judgments about the two components. The pattern of excitatory interactions and near-perfect correlated noise demonstrates instead that observers are primarily basing their judgments on a linear combination of responses across the disparate frequency bands. These results support the general notion of edge detectors in human vision, and are consistent with our own quantitative formulations.

◆ **Isolating excitatory and inhibitory nonlinear spatial interactions involved in contrast detection**

B Zenger, D Sagi (Department of Neurobiology/Brain Research, The Weizmann Institute of Science, Rehovot 76100, Israel)

By using psychophysical experiments and models we explored patterns of nonlinear interactions between different spatial channels. In particular, we studied excitatory and inhibitory interactions between filters of different orientations and spatial locations. A two-alternative forced-choice procedure was used to measure detection thresholds for masked Gabor signals. Mask elements were two Gabor signals of equal contrast (either same or opposite phase) differing from the target element either in orientation ($\pm \Delta\theta$) or in spatial location ($\pm \Delta x$). Detection thresholds were measured as a function of mask contrast for different target-to-mask distances ($\Delta\theta$, Δx). When masks were presented at different orientations or at close spatial distances ($< 3\lambda$) these functions typically had a minimum at a nonzero mask contrast, thus showing facilitated detection in the presence of the mask. The magnitude of this facilitation (up to 0.4 log units) decreased with increasing target-to-mask distance. No facilitation was observed when masks were of opposite phase. A different pattern of data was obtained for masks presented at larger spatial distances. Here, a sensitivity enhancement was found (0.1 log units) which increases monotonically with mask contrast and is independent of mask phase.

These results cannot be accounted for by a single-filter model. We suggest a model in which nonlinear interactions between different filters are assumed. Facilitation by low-contrast masks of the same phase can be explained by linear subthreshold summation of mask and target contrast within a single filter. However, observed facilitation is in most cases smaller than expected from the single-channel model. We assume isotropic inhibitory interactions between channels of different orientations and different (neighbouring) spatial locations, which account for threshold elevations in the presence of high-contrast masks and for the reduced facilitation. Further, we suggest anisotropic excitatory interactions which lead to phase-independent sensitivity enhancement by masks presented at larger spatial distances.

◆ **Pattern-contrast discrimination by ON and OFF pathways**

R W Bowen (Department of Psychology and Parmlly Hearing Institute, Loyola University, Chicago, IL 60626, USA)

We analyzed contributions of ON and OFF pathways to contrast discrimination. The base contrast (C) was a cosine pattern, 3 cycles deg^{-1} , 500 ms duration. The added contrast (ΔC) was a D6 pattern (sixth derivative of a Gaussian), also 3 cycles deg^{-1} , 30 ms duration. We manipulated the polarity of ΔC (incremental or decremental) and phase of C (light or dark bar). The brief ΔC was coincident with either the onset or the offset of the longer C . At onset of a

light bar of the cosine, discrimination of a positive D6 follows a 'dipper' function: a dip in ΔC at low C and a power relation ($n < 1$) at high C . For a negative D6, however, ΔC rises at low C values and remains elevated from positive D6 thresholds at high C values. The inverse occurs at offset of a light bar—a dipper for negative D6s and a rise in ΔC for positive D6s. Reversing the phase of C to a dark bar also reverses all ΔC -to- C polarity interactions at both onset and offset of C . We assumed an accelerated contrast response at low C values and analyzed alternative schemes for detection in the pathways. For example, for a negative ΔC at the onset of a positive C , was detection by the OFF pathway or by a decrease in ON-pathway activity? We infer that positive and negative polarities of ΔC are detected in ON and OFF pathways, respectively, whether C is same or opposite polarity. For opposite sign of ΔC and C , we observe subtractive opponency between ON and OFF pathways at low C values: $|\Delta C| - |C| = K$, where K is the unmasked threshold. At high values of C , the interaction of ON and OFF pathways appears to be divisive in nature: discrimination functions for positive and negative ΔC are governed by the same power-law exponent.

◆ Effects of spatial-frequency uncertainty on signal-detection behaviour

R Hübner (Institut für Psychologie, Technische Universität Braunschweig, Spielmannstrasse 19, 38106 Braunschweig, Germany)

If the spatial frequency of sinusoidal signals in a signal-detection experiment varies randomly from trial to trial, then performance is decreased compared with that in a situation where the spatial frequency is constant. However, this spatial-frequency-uncertainty (SFU) effect can more or less be compensated by presenting informative cues shortly before each trial.

Several models have been proposed to explain the effects of SFU [cf Graham, 1989 *Visual Pattern Analysers* (New York: Oxford University Press)]. While in multiple-band models it is assumed that under SFU several spatial-frequency-specific channels are monitored simultaneously, in single-band models it is proposed that attention switches from channel to channel. If cues are provided, the models predict that the number of monitored bands or switching, respectively, is reduced. Up to now it is open which of these models is valid. However, as recent results (Hübner, 1993 *Biological Cybernetics* 69 457–462) demonstrate, considering psychometric functions can help to distinguish between them. Therefore, psychometric functions were collected in a signal-detection experiment under conditions of constant spatial-frequency, SFU, and cueing. It turned out that the amount of the SFU effect varies systematically with spatial frequency. This result can well be explained by a multiple-band model, as a quantitative analysis reveals. Further, the results suggest that cues not only affect the number of monitored channels but also their output variance.

◆ Contrast-increment thresholds measured at various levels of external spatial noise

K M Tiippana, J M Rovamo, R E Näätänen† (Department of Vision Sciences, University of Aston, Birmingham B4 7ET, UK; †Department of Physiology, PO Box 9, University of Helsinki, Helsinki SF-00014, Finland)

Contrast-increment thresholds were measured for cosine gratings of 4 cycles deg^{-1} with areas of 0.0625 and 16 deg^2 at pedestal contrasts of 0.625%–10% without external noise and with various levels of external spatial noise. The results were expressed by means of two measures, Michelson contrast and contrast energy. Michelson-contrast-increment thresholds were calculated as $\Delta C = C_{\text{tot}} - C_{\text{ped}}$, where C_{tot} is the total contrast of the pedestal and increment and C_{ped} is the contrast of the pedestal. Contrast energy was calculated by $E = \sum \sum c^2(x, y) p^2$, where $c(x, y) = [L(x, y) - L_0]/L_0$. $L(x, y)$ is the luminance distribution of the grating, L_0 is its mean luminance, and p^2 is the area of a pixel in solid degrees. Contrast-energy-increment thresholds were calculated as $\Delta E = E_{\text{tot}} - E_{\text{ped}}$, where E_{tot} is the total energy of the pedestal and increment, and E_{ped} is the energy of the pedestal. When Michelson-contrast-increment thresholds were plotted as a function of pedestal contrast, the resulting contrast-discrimination curves were mostly dipper shaped. At low pedestals, contrast-increment thresholds decreased below the detection threshold, but at high pedestals they increased with pedestal contrast. Increasing the spectral density of noise increased detection thresholds and caused the dip in the contrast-discrimination functions to shift to higher pedestal contrasts. When increment thresholds were expressed as contrast-energy-increment thresholds, the shape of the discrimination functions changed so that, with increasing pedestal energy, the increment thresholds first remained constant and then started to increase, falling on a straight line in double logarithmic coordinates. When energy-increment thresholds and pedestal energies were normalised by the detection threshold, all data measured at different noise levels and grating areas fell together and formed a single function. It was first constant and then followed a power function with an exponent of 0.86.

DEVELOPMENT AND AGING

◆ Development of chromatic sensitivity along cone-isolating axes

K Knoblauch, F Vital-Durand, J Barbur† (INSERM Unité 371, Cerveau et Vision, 69500 Bron, France; †Centre for Applied Vision Research, The City University, London EC1V 0HB, UK)

Although several studies have documented the presence and functioning of colour-vision mechanisms within the first four months after birth, little is known about their rate of development afterwards and the point at which chromatic sensitivity approaches adult levels. We have attempted to fill this void by measuring thresholds for chromatic differences in individuals ranging from 4 months of age to adulthood, using a common apparatus for all ages. A two-alternative forced-choice procedure was used to estimate the minimum chromatic displacement that could be detected along the dichromatic confusion lines from the point (0.305, 0.323) in the CIE x, y chromaticity diagram. These axes in colour space correspond to directions that isolate each cone class in turn. Test stimuli were presented in one of two spatial locations as a set of three bars alternating in orientation between vertical and horizontal on a pedestal of spatiotemporal random luminance noise. The purpose for the noise was to mask detection based on luminance differences that might arise because an individual differed from the CIE standard observer. Colorimetric purity of the bars was varied between trials to estimate the threshold for detecting their presence. For individuals younger than 2 years, thresholds were measured by using a preferential-looking technique. For older individuals, responses were obtained verbally or by pointing. Data collected from a sample of fifty individuals show that between 4 months and 10 years of age the sensitivity of each class of cones increases at a similar rate by about a factor of 20. These results suggest that colour vision varies quantitatively but not qualitatively over age.

◆ Developmental changes and learning in texture segmentation

R Sireteanu, R Rettenbach (Max-Planck-Institut für Hirnforschung, Deutschordenstrasse 46, 60528 Frankfurt, Germany)

Texture segmentation, assessed with a forced-choice preferential-looking technique, develops late in childhood (Sireteanu and Rieth, 1992 *Behavioral Brain Research* 49 133–139). In the present study, we investigated the development of texture segmentation in schoolchildren, by using a method of manual reaction time. The subjects were presented with a matrix of 20×20 obliquely oriented line elements on a computer screen. A discrepant element or a group of sixteen discrepant elements could be presented at the centre, on the right, or on the left side of the display. One quarter of the trials did not contain a target. The subjects' task was to press the button of the computer mouse as soon as they detected the target, then to indicate whether and where the target had been. One hundred schoolchildren between 6 and 20 years of age and twenty naive adult observers participated in the experiments. For the adult observers, the response time to the discrepant targets was always identical to the response time to single, clearly visible items (basic reaction time). This confirms that, for these subjects, texture segmentation is preattentive. During the first experimental runs, response time to the homogeneous displays was longer than to the displays containing a target but showed a substantial decline in subsequent presentations. This improvement of performance with practice can be interpreted as a form of perceptual learning. For children in the youngest age groups, reaction time to a single discrepant line or a discrepant group of lines was higher than the basic reaction time. The difference decreased and, in some cases, disappeared completely with practice. These results indicate that, for young, unpractised schoolchildren, the segmentation of textures requires processing time, and therefore cannot be called preattentive. Thus, we confirmed the findings of Sireteanu and Rieth (1992). In addition, we showed that, both for schoolchildren and for adults, initially serial processes can become parallel with practice.

◆ Reconstruction of visual perceptual image by children with normal and poor vision

I V Blinnikova, M E Bernadskaya (Laboratory of Neuropsychophysiology, Institute of Curative Pedagogy, Pogodinskaya 8, 119834 Moscow, Russia)

Changes of strategies for the reconstruction of visual perceptual images by children aged 5 to 12 years with poor and normal vision were investigated. The task of those tested was to complete twelve pictures with missing parts, in three trials of different complexity, when viewing the complete models. Pictures had several levels of complexity, from simple geometrical figures to complicated drawings. Children's mistakes and ways of accomplishing the task were analysed. The youngest children with normal vision reconstructed the pictures on the basis of separate parts, whereas the older children used the strategy of reconstruction based on the holistic image. Pictures drawn by the children with poor vision allow us to add to these data

and to reconsider the process of reconstruction of the visual image, which can be divided into four age stages. Depending on the stage, the reconstruction was either based on (a) the holistic (undivided) image; (b) separate parts; (c) the holistic (generalised) image; or (d) the detailed image. These stages may be reduced to two cycles. In each of these cycles the reconstruction based on elements of the pictures comes after the reconstruction based on the whole image.

We tried to find a correlation between these results and the well-known data obtained by J Piaget and B Inhelder [1948 *La Représentation de l'Espace chez l'Enfant* (Paris)]. Though it may sound paradoxical, these results are correlated with results obtained in investigations devoted to the microgenesis of the visual perceptual image, which is unfolded during 300 ms after display of the stimulus [(Velichkovsky, 1982, in *Cognitive Research in Psychology* Eds F Klix, J Hoffmann, E Van der Meer (Amsterdam: Elsevier)]. This correlation enables us to determine the general tendency of visual development.

LEARNING AND MEMORY

◆ Improvements in contrast sensitivity and in the detection of low-contrast stimuli: studies of 'low-level' perceptual learning

P T Sowden, I R L Davies, D Rose (Department of Psychology, University of Surrey, Guildford, Surrey GU2 5XH, UK)

Several recent studies (eg Fahle and Edelman, 1993 *Vision Research* 33 397–412) have shown 'low-level' perceptual learning. In these studies it is suggested that visual processing may be more 'plastic' at a neural level than had previously been suspected. We report two experiments in which we investigated this low-level plasticity further. In experiment 1, observers completed 10,000 temporal forced-choice signal-detection trials for a sine-wave grating. Results showed a trend for an improvement in contrast sensitivity over the course of training. This improvement was specific to the trained eye and to the retinal location of the training stimulus. Further, follow-ups revealed that the trend for improvement continued for two months after training and then remained stable for a further four months.

In experiment 2, observers' eye dominance and their contrast sensitivity for each eye was assessed. Observers then took part in a spatial forced-choice signal-detection task for high-spatial-frequency, low-contrast stimuli. After baseline measures for each eye, observers completed 8 days training using only their nondominant eye. Baseline measures showed superior detection times for observers' dominant eye. Results showed a trend over the course of training for improvements in the time taken to detect the holes. At least some of this change appeared to be specific to the trained eye and thus to occur at a low level.

◆ Changes in macaque inferotemporal neuron responses during learning of a visual task

V Yakovlev, S Hochstein (Neurobiology Department and Center for Neural Computation, Hebrew University, Jerusalem 91904, Israel)

Inferotemporal (IT) cortex of monkeys plays a crucial role in learning visual discrimination tasks. In previous studies only the 'before' and 'after' learning conditions were tested. We now measure responses during the learning of the task and ask if the activity of IT cortical cells changes from session to session while the monkey's performance improves.

Multiple single-unit recordings were taken from IT cortex of a macaque monkey performing a standard match-to-sample task. The stimuli were a bright solid circle and rectangle, of equal area and energy. We studied the responses of IT cells in all stages of learning, from the level of chance performance to 90% correct responses. For analysis, the learning period was divided into three stages: I chance performance; II ~60% correct responses; and III >60% correct responses.

We found that the most dramatic changes in activity of IT cells occurred as the monkey progressed from stage I to stage II. For the Same condition, in stage I the activity was greater during the first, Sample, stimulus than during the second, Match, stimulus, whereas at later stages the response to the Match stimulus grew in size. The activity of cells during the inter-stimulus interval in stage I was suppressed compared with background activity, whereas later it was generally stronger than background, even surpassing the response during the stimulus, implying they may be involved in remembering the Sample. Finally, in stage I, responses of IT cells to the Match stimulus were suppressed for the Match condition compared with the Nonmatch condition. In later stages the Match response grew in size and presumably in importance. Thus, specifically, the memory aspect of IT cells develops during learning.

◆ **Categorical distribution of memory-matched colors in the OSA uniform color space**

K Uchikawa, T Sugiyama, H Ujike (Department of Intelligence Science, Tokyo Institute of Technology Graduate School, 4259 Nagatsuta, Midori-ku, Yokohama 227, Japan)

Memory color-matching was carried out to see how colors we remember are distributed in a color space. If color appearance did not change in memory, characteristics of the matching distribution would be the same as those obtained by simultaneous color-matching. However, if colors in memory are organized differently from the simple color-difference basis, the distribution of memory-matched colors should reflect this structure of color memory.

We produced 1355 colors on a color CRT so that they simulated the real OSA uniform color chips and interpolated between them. We chose 203 test colors uniformly distributed in even numbers of lightness levels of the OSA color space. The observers saw a test color for 5 s to memorize it. Then, 30 s later they started changing colors on the color CRT to obtain a memory-matched color in the OSA color space. The observers repeated this memory color-matching five times for a test color. Each observer also performed categorical color naming for all 1355 colors more than twice with Berlin and Kay's 11 basic color names (red, green, yellow, blue, brown, purple, orange, pink, white, black, and gray) to determine categorical color regions in the color space. Each categorical color region was defined as an area consisting of colors consistently named with a certain basic color. The results obtained for three observers clearly show that memory-matched colors did not uniformly spread around each test color, but made several clusters in the OSA color space. It seems that a cluster is included in a single categorical region of the 11 basic colors, which indicates that colors are somehow categorically organized in memory. It is suggested that there is some physiological mechanism for categorical color perception in a high level of color vision.

MINI SYMPOSIUM: PERCEPTION OF COMPLEX IMAGES

◆ **Pictorial relief**

J J Koenderink (Utrecht Biophysics Research Institute, Utrecht University, 3508 TA Utrecht, The Netherlands)

'Pictorial relief' is part of your experience when you look at a flat picture and 'see' a scene that is articulated in the depth domain. Because of its importance for the artist there have been, from Renaissance times, theoretical treatises on relief, culminating in the influential book by the sculptor Adolf Hildebrand from 1893. For the empirical sciences pictorial relief has remained a somewhat elusive phenomenon. In daily life pictorial relief is of tremendous importance, of course. It is also of considerable scientific and perhaps even philosophical interest, as is indicated by synonyms such as 'paradoxical stereopsis' found in the literature. Ways to define pictorial relief operationally are considered and results presented on pictures of geometrically nontrivial shapes such as pieces of sculpture or human torsos. Issues of intraobserver consistency, interobserver variability, veridicality, and dependence on viewing conditions are addressed.

◆ **Visual perception as Bayesian 'inference'**

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A framework is described for characterising perception as Bayesian inference and analysing its implications for the investigation and computational modelling of human visual perception. The Bayesian approach suggests new ways to conceptualise the general problem of perception and to decompose it for psychophysical investigation. It not only provides a framework for modelling solutions to specific perceptual problems, but also guides the definition of the problems. In particular, it provides the foundation for a well-defined 'psychophysics of constraints' in which one tests hypotheses regarding quantitative and qualitative constraints used in human perceptual inferences. This analysis will be applied to the perception of three-dimensional object motion from cast-shadow motion. A major advantage of a Bayesian approach is that, because its structure is the same as that of the Bayesian framework for computational modelling, it supports a strong integration of psychophysics and computational theory. More generally, a Bayesian perspective unifies many aspects of computational, ecological, and Gestalt approaches to perception.

◆ **The successes and failures of colorimetric reproductions**

J J McCann (Vision Research Laboratory, Polaroid Corporation, Cambridge, MA 02139, USA)

We have studied a process of making actual-size reproductions of great paintings by photographing the original painting with a calibration target, scanning the image, and using the data

from the calibration target to transform the printed image to be a colorimetric match to the original. The process works well as long as the color gamut of the printing medium is approximately equal to that of the original.

When the gamuts differ by a great deal, such as CRT and print gamuts, or real-life scenes and print gamuts, noncolorimetric transformations are required. The range of radiances in real-life scenes are compared with those available in print and display media. As well, a variety of different noncolorimetric transforms are discussed.

◆ **Perceptual image quality: linking psychophysics and image technology**

J A J Roufs (Institute for Perception Research, PO Box 513, 5600 MB Eindhoven, The Netherlands)

In the last decade visual psychophysicists and image technologists have learned to understand each other's terminology and concepts and have stimulated each other to their mutual benefit. The keyword characterising the common interest is perceptual image quality, which expresses a degree of excellence. As was argued earlier (Roufs and Bouma, 1980 *Proceedings of the SID* volume 21/3, pp 247-270; Roufs, 1992 *Philips Journal of Research* 47 35-62), it makes sense to distinguish between appreciation-oriented and performance-oriented image quality. Both are complex psychological attributes which result from underlying simple attributes such as sharpness or brightness contrast. Perceptual quality and the strength of the underlying attributes have to be measured in order to relate them in a technically meaningful way to the physical parameters. Although thresholds do provide valuable information, emphasis has to be put on suprathreshold vision. This implies scaling of the various psychological attributes involved.

The state of the art in image processing makes it possible to make certain quality dimensions dominant and to vary their strength in order to establish their relation with perceptual image quality. Examples are given. Tests of the validity of different scaling methods are discussed. Owing to the specific types of measurements, certain issues, such as representativeness and repeatability of measurement, the necessity of references in the case of judgment in different sessions, and the relations between the rating of experts and laymen, are relevant and are commented upon. Efficient coding and technical limitations cause various image degradations. The summing effect of different types of degradations has been modelled. The established simple relation with perceptual image quality is discussed. Adequate image description and intelligent coding provide interesting possibilities to evaluate the effect of scene-determined quality aspects. Examples are given. Local changes in perceptual attributes become possible. Moreover, this approach enables one to perform 'analysis by synthesis', a technique which has been successful with respect to the processing of the one-dimensional signals in speech technology. It brings nearer the establishment of equations which describe the relations between perceptual quality, the strength of its underlying dimensions, and the physical image parameters. In the end these relationships have to be based on the properties of an internationally agreed standard observer, as was accomplished in the case of light. Such an equation would make much ad hoc research on image quality superfluous. The desirability and usefulness of this kind of approach is discussed. Finally, some examples of modern developments in image technology in appreciation- and performance-oriented environments are given and speculations are made as to their effect on the research in visual psychophysics.

INVITED LECTURE: COLOUR PERCEPTION

◆ **Color appearance and the control of chromatic adaptation**

LT Maloney (Center for Neural Science and Department of Psychology, New York University, New York, NY 10003, USA)

In his 1961 address to the Spanish Royal Society, W S Stiles suggested that the study of color vision be considered as the study of two processes, local retinal adaptational state and the process that selects the local state, the control of adaptation. First, recent work concerning the chromatic pathways that determine color appearance and the chromatic pathways that control the adaptational state of the appearance pathways is reviewed. Then recent color-constancy algorithms viewed as models of adaptational control are discussed. Last, recent work is summarized that concerns the interaction of the spatial and temporal characteristics of stimuli and their color appearances, and how these interactions can be used to identify chromatic mechanisms.

COLOUR PERCEPTION

◆ Cone fundamentals: molecular genetics and psychophysics

A Stockman, LT Sharpe[†], J Nathans[#], A Reitner[§] (Department of Psychology, University of California at San Diego, La Jolla, CA 92093-0109, USA; [†]Neurologische Universitätsklinik, 79104 Freiburg i. Br., Germany; [#]Howard Hughes Medical Institute, Johns Hopkins University School of Medicine, Baltimore, MD 21205, USA; [§]II. Universitäts-Augenklinik, 1090 Wien, Austria)

The derivation of König cone fundamentals depends on the spectral sensitivities or matches of true reduction-type dichromats. Molecular genetics now allows us to identify the appropriate dichromats; ie those whose X-chromosome carries a single gene in the red-green tandem array, either one of the two polymorphic variants of the normal red-pigment gene, R(ala¹⁸⁰) or R(ser¹⁸⁰), or a de facto normal green-pigment gene, the hybrid gene R1G2. Accordingly, we have measured the red-cone spectral-sensitivity functions in fourteen R(ala¹⁸⁰) and seven R(ser¹⁸⁰) observers and the green-cone functions in four R1G2 observers (and in two R2G3 observers, whose hybrid gene produces a pigment that is essentially identical to that produced by the normal green-pigment gene), by repeatedly measuring their foveal (2 deg) heterochromatic brightness curves by means of the minimal-flicker method. A reference light (560 nm) was alternated at a rate of 16 or 25 Hz, in opposite phase with a superimposed test light, the wavelength of which was varied in 5 nm steps over the spectrum from 400 to 680 nm. To saturate the rods and to prevent the blue cones from contributing to the curves, the flickering stimuli were superimposed on a large, violet (430 nm) background with an intensity of 11.5 log quanta s⁻¹ deg⁻². Estimates of each observer's lens and macular-pigment densities were also obtained psychophysically. Preliminary data show that the red-cone spectral sensitivities measured psychophysically in the R(ala¹⁸⁰) and R(ser¹⁸⁰) dichromats differ in spectral position by ~4 nm, in accordance with absorbance measurements of pigments constructed from DNA clones (Merbs and Nathans, 1992 *Nature (London)* **356** 433), whereas the green-cone spectral sensitivities are consistent with previous measurements. These dichromatic spectral-sensitivity measurements, along with measurements of blue-cone spectral sensitivities that are in progress, will allow the derivation of König cone fundamentals that accurately represent the two major polymorphic variants of human colour vision.

◆ Can a model of color discrimination account for color appearance in the equiluminant plane?

V C Smith, J Pokorny (Visual Science Center, University of Chicago, Chicago, IL 60637, USA)

Chromatic discrimination and color appearance were evaluated with surrounds of differing chromaticity in the equiluminant plane, by using stimuli expressed in S, M, and L cone trolands. Stimuli and surrounds were created by means of a PIXAR image-processing system and were presented on a CRT. Stimuli were (a) ten test colors on a contrast S cone troland line (their surrounds matched the tests in L tds but were at different S tds); (b) ten test colors on a constant L troland line (their surrounds matched the tests in S tds but were at different L tds). The test lines intersected at equal-energy-white (EEW). Tests were 0.9 deg squares; surrounds were 2.7 deg × 8.1 deg rectangles; the retinal illuminance was 115 effective tds. Three observers matched each test-surround combination to a comparison color presented in an EEW surround. Test and comparison were presented to separate eyes in a haploscope. Color-discrimination data were collected for the test stimuli and fitted to a discrimination model based on the response properties of the parvocellular pathway. There was induction away from the surround (except for white). With a white surround, the matches fell on a 45° line intersecting EEW. For L-troland tests, as the surround color varied in L tds from neutral, L matches fell on two 45° lines separated by a hiatus. One line showed constant, maximal induction as predicted by the chromatic-discrimination model. The other line showed constant minimal induction. In the hiatus, the level of induction decreased but the dominant hue percept varied only in S-cone content. Analogous results were obtained for S-troland tests. The data suggest that neither the red-green nor the blue-yellow chromatic opponent systems represent unitary mechanisms.

◆ Illuminant invariants at receptor and postreceptor levels as a basis for relational colour constancy

S M C Nascimento, D H Foster (Department of Communication and Neuroscience, Keele University, Keele, Staffs ST5 5BG, UK)

One aspect of colour constancy concerns the ability of an observer to classify correctly colour transformations of scenes as either consistent or inconsistent with changes in the spectral composition of the illumination (Foster et al, 1992 *Ophthalmic and Physiological Optics* **12** 157-160). The mechanisms underlying this ability have been assumed to encode visual

information in such a way that intercolour relationships are preserved. Although an empirical measure of these relationships was found to be consistent with performance (Nascimento and Foster, 1993 *Perception* 22 Supplement, 57), it is unclear whether the visual system has access to the necessary invariant signals. This question was addressed here by modelling, at receptor and postreceptor levels, the stability of possible invariant cues.

Cone-receptor excitations were estimated for surfaces under pairs of different illuminants, and colour-vision models by Hunt and Guth applied to estimate the corresponding post-receptor signals. Surfaces could either be simulations of Munsell chips selected randomly from 1257 samples or have randomly generated spectral reflectance functions. Illuminants were simulations of phases of daylight illumination drawn at random from the daylight locus, or simulated blackbody radiators with temperatures drawn at random from the range 2000 K–10000 K, or simulations of sources with randomly generated spectral distributions.

At the receptor level, ratios of cone excitations produced by different surfaces were almost invariant under illuminant transformations; this result held statistically and was robust even when surfaces were spectrally random. At the postreceptor level, differences between opponent-colour signals were more stable than their ratios. In either case, the visual system appears to have access to combinations of signals which remain almost invariant under illuminant transformations and which can therefore provide sufficient information for relational colour constancy.

◆ Colour constancy under natural and artificial illumination: a test of models

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Colour constancy was studied under natural and extremely artificial illumination. Four test illuminants were used: two broad-band phases of daylight (correlated colour temperatures 4000 K and 25000 K) and two spectrally impoverished metamers of these lights, each consisting of only two wavelengths. Computer simulation was used for reproducing the chromaticities and luminances of an array of Munsell colour samples, as rendered under the different test illuminants. An asymmetric haploscopic matching paradigm was used in which the same stimulus pattern, illuminated either by one of the test illuminants or by a standard broadband daylight (D65), was alternately presented to the left and right eye. The results show the (expected) failure of colour constancy under two-wavelengths illumination, and approximate colour constancy under natural illumination. Quantitative predictions of the results were made, by means of a model based on cone-specific contrast processing (Lucassen and Walraven, 1993 *Vision Research* 33 739–757). In addition, we derived predictions on the basis of two different computational approaches, respectively aiming at recovering reflectance (from small-dimensional linear models), or generating 'smoothest reflectance' functions (van Trigt, 1990 *Journal of the Optical Society of America A* 7 1891–1904). It was found that the two latter models yield somewhat less-accurate predictions than the cone-contrast model, particularly for the conditions in which the samples are shown under natural illumination.

◆ Two modes of appearance: aperture color and surface color

T Indow (Department of Cognitive Sciences, University of California at Irvine, Irvine, CA 92717, USA)

Colors we perceive under natural condition are predominantly surface mode (S) whereas most psychophysical data are obtained with colors of aperture mode (A). These two modes of appearance stem from the same local stimulation in the retina and the difference is due to the excitation condition of the surrounding area. Interchangeability of psychophysical laws between the two modes are discussed. (1) Color discrimination ellipsoids, except yellow, are the same in the CIE color space if defined by the method of adjustments, similar but different in size if defined by the method of constant stimuli (Indow and Morrison, 1991 *Color Research and Application* 42–56; Indow et al, 1992 *Color Research and Application* 6–23). (2) Curves for opponent processes, R–G and Y–B, for monochromatic lights (A) as functions of wavelength and those for most saturated surface colors (S) as functions of dominant wavelength are fairly similar. The similarity of the curves gives us information on the extraspectral region, eg Munsell P is shown to consist of R and B. (3) Brightness changes as a function of Y (cd m^{-2}) in A from dark to bright, whereas it changes as a function of reflectance $Y\%$ in S from black to white. This is the reason why some color names, eg brown, do not exist in A. (4) Change of saturation as a function of colorimetric purity (A) and change of Munsell chroma (S) will be compared.

◆ New effects of response nonlinearity on colour perception

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Visual response nonlinearity plays an important role in colour perception. The Bezold-Brücke hue shift, for example, is caused by such nonlinearity, and electrophysiological evidence supports the idea that cone photoreceptors and other postreceptoral cells show compressive response nonlinearity. We have found new psychophysical effects which relate to the response nonlinearity more directly and propose a model to explain these effects.

We measured brightness, hue, and saturation of flickering monochromatic lights with small duty ratio (0.1) and high retinal illuminance (average 4000 Td) as a function of flicker frequency (ranged from 30 to 60 Hz). It is expected that such a stimulus undergoes response nonlinearity at its peak whereas a steady light with the same average energy as the flickering light does not undergo the nonlinearity. The effects of response nonlinearity were revealed by comparing brightness, hue, and saturation of the flickering stimulus and those of the steady stimulus. Two colour-normal subjects participated in the experiments. The results showed that the brightness of the flickering stimulus was diminished at around 30 to 40 Hz, that the hue shifted toward the same direction as Bezold-Brücke hue shift as frequency decreased, and that the saturation was decreased as frequency decreased, except for long wavelengths. As the flicker frequency increased, the effects became less prominent and they almost disappeared at higher frequencies than the critical flicker frequency as predicted by the Talbot-Plateau law. We propose a model based on the response nonlinearity of the cones to explain the results. A low-pass feature of the cone temporal-modulation transfer function and sigmoidal nonlinearity of the cone response were assumed in this model.

APPLIED PSYCHOPHYSICS

◆ Visual temporal masking at scene cuts

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In the present work we extended classical studies of temporal masking to naturalistic images by investigating the sensitivity of the human visual system to video coding artifacts following a scene cut. On the basis of known properties of the human visual system, we might expect that coding artifacts would be concealed by forward masking for up to 100 ms (or about 2–3 video frames) after a scene cut. With reference to classical studies of masking, the video frames preceding the scene cut would function as a mask, while the coding artifacts in the frames following the scene cut would function as the signal. A set of image sequences, each 2 s in duration, were selected for study. Each sequence had a cut at the 1 s mark, such that the image content was different in the first half from in the second half of the sequence. The severity of coding artifacts in video frames immediately following the cut was varied systematically. The level of impairment that resulted in 75% correct identification (two-alternative forced-choice procedure) of the image coding artifacts was estimated using psychophysical procedures (PEST and method of constant stimuli). This estimation of sensitivity was done independently for the 1st, 2nd, 3rd, and 4th frames following the scene cut, and for a combination of frames following the cut.

It was found that visual masking effects were present in the first frame following a scene cut, but diminished markedly in subsequent frames and were virtually absent by the third or fourth frame. The visibility of image-coding artifacts depended on the local structure of the image and was not uniform throughout the image. Forward masking effects occur at scene cuts in naturalistic video image sequences. These effects permit the bit-rate to be reduced after a scene cut because forward masking will conceal the resulting coding artifacts.

◆ Discrimination of time to contact in the central and peripheral visual field

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Timing of interceptive acts is generally considered to be based upon visual information concerning the time remaining until the object reaches the observer ('time to contact'). This optical variable (named tau) is equal to the ratio between the angular size and the rate of expansion of the object. Perceiving time to contact involves extracting the information contained in the optic flow. In the present experiment we examined whether the ability to perceive time to contact was equivalent in central and peripheral vision.

We simulated rectilinear motion in the depth of a ball, which was on a collision course with the observer. Visual stimulations were projected on a large screen in front of the subjects.

Times to contact, ranging from 1.6 to 2.4 s, were obtained by varying the approach velocity of the ball. Only the first second of the trajectory of the ball was visible, and subjects had to decide whether the ball would arrive sooner or later than the mean of the stimulus set. Subjects were first trained and tested in central vision. After that, the same stimulations were presented at 5, 10, and 20 deg of eccentricity. In these conditions, subjects had to fixate a central point. Fixation was controlled by recording horizontal eye movements by means of an infrared reflection device. Head movements were also restrained, by means of a dental-impression bite bar. Viewing was binocular. Results from eight subjects showed that performance in central vision is better than that in peripheral vision. The foveal and the peripheral part of the retina do not seem to be equivalently efficient for the extraction of tau. During unrestricted vision, performance was equivalent in the central and peripheral visual field, suggesting that saccadic eye movements toward peripheral stimuli might be necessary to enable correct perception of time to contact.

◆ **The estimation of time to contact with a computer-generated image**

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When driving a car it is of vital importance that drivers are able to time their actions accurately. Estimating when objects will be reached (the time to contact or TTC) is fundamental to many driving tasks. Visual information will be the drivers' primary source of TTC information.

In a driving simulator, the drivers' TTC estimates should resemble their real-world behaviour as much as possible. The computer-generated image (CGI) in a driving simulator is limited with respect to the complexity of the scene and the resolution of the display. In an experiment, the effect of scene complexity on the estimation of TTC was investigated with a three-channel 150 deg × 40 deg CGI with a resolution of 600 pixels × 800 pixels per channel. Three motion conditions were simulated: observer motion, object motion, or both. The results for the object-motion condition confirm the results of Shiff and Detwiler (1979 *Perception* 8 647-658), who found no effect of scene complexity on the estimates of a stationary observer. The results for moving observers show that TTC estimates are more realistic in complex visual scenes. The results further indicate that the resolution of the CGI is insufficient for the perception of the TTC of objects with a small visual angle (small and/or distant objects).

◆ **Estimation of perceived blur in images**

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Blur is an important and widespread degrading factor in images. It has been shown that the spread of the blurring kernel is a good objective correlate of the unsharpness of images (Westerink and Roufs, 1989 *SMPTE Journal* 98 113-119). Hence, by estimating the spread of the blurring kernel from a blurred image, its unsharpness (or perceived blur) can be predicted, which can then be used to predict image quality.

The results of estimation of the spread of the blurring kernel from images by means of a computational algorithm and the results of correlation of these estimates with subjectively judged blur are reported. The objective estimates of blur spread are obtained from the blurred image by using a computational algorithm which involves estimation of (local) blur spread at many prominent edge locations in the image, the prominence being decided by both the edge height and the length of the edge segment, and combining the local edge-blur information at all prominent edge locations to form a global estimate of blur spread. Estimates at edges are obtained by analysing the image by using a polynomial transform. Polynomial transforms have many properties in common with the early stages of the human visual system (Martens, 1990 *IEEE-ASSP* 38 1595-1606).

In a psychophysical experiment subjects were asked to judge the blur of the images by using a category scale. Two natural scenes and one synthetic scene were used. Sixteen stimuli of each scene were created, containing four levels of blur spread and four levels of noise. Images were blurred by convolving with Gaussian kernels. Stimuli containing noise were included to study the effect of noise on perceived blur. The objective estimates of blur spread for each stimulus were obtained by applying the algorithm to each stimulus. The results of the subjective blur were correlated with the estimates of the blur spread. This resulted in a very good correlation for the three scenes.

- ◆ **Measuring the effectiveness of image-enhancement techniques in terms of visibility distance**
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To monitor telerobotic maintenance and service operations on Freedom Space Station, image-enhancement techniques will be used to cope with the intense glare or almost total shadow of the visual environment in space. We tested whether visibility distance could be used to determine quantitatively which enhancement techniques are optimal in various situations. Video images were taken of 1:72 scale models of the shuttle Atlantis, the European Space Lab, and a communication satellite in illumination conditions that produced varying degrees of glare and shadow. No enhancement, a brightening function, a darkening function, edge finding, and histogram equalization were introduced into these images and presented on a high-resolution computer display. The display was moved at a speed of 0.18 m s^{-1} towards and away from an observer seated at one end of a 7.3 m automated test track. A parallax-free binocular-viewing device eliminated stereoscopic distance cues. The method of limits was used to measure the distance at which observers could discern certain features of each of these objects. The image enhancement that led to the longest visibility distance varied significantly depending on the feature to be discerned and the lighting conditions. We conclude that visibility distance is an effective means of determining which image-enhancement technique is optimal under a variety of circumstances, and that such measurements could be used to establish guidelines for use of these techniques.

ATTENTION, VISUAL SEARCH, AND EYE MOVEMENTS

- ◆ **Orienting and reorienting of visual attention before express saccades**
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Fischer and Weber (1993 *Brain and Behavioral Sciences* 16 553–610) defended a model of saccade generation according to which attention disengagement is necessary for the preparation of express saccades (visually guided saccades with latencies around 100 ms). To evaluate this model exogenous and endogenous cues were used to orient attention to a particular location before the onset of the target for the saccade. Target location was randomised between 4 deg to the right or left; cue validity was 75% (1280 trials per subject in each paradigm). The two possible target locations were surrounded with a large box. The exogenous cue was a 40 ms flash of one of the boxes; in one paradigm the fixation stimulus remained on during the trial (fixation-overlap), in another paradigm the fixation stimulus was removed 200 ms before target onset (fixation-gap). The endogenous cue was a central arrow that indicated one box and that remained on until the end of the trial. On the basis of previous experiments with 100% valid cues, the times between cue and target onset were chosen to yield a large number of express saccades.

In confirmation of earlier results, valid cueing of the location for the saccade did not interfere with the preparation and execution of express saccades. Invalid cueing, however, precluded express saccades in all paradigms: subjects produced either fast-regular (latency around 150 ms) or slow-regular (latencies higher than about 190 ms) saccades to the target or they executed an (anticipatory) saccade to the cue. In the case of the cue-elicited saccades in the invalid trials, continuous amplitude-transition functions were found: starting at about 60 ms from target onset, the amplitude continuously decreased from 4 deg to values below 1 deg. The present findings necessitate a revision of Fischer and Weber's (1993) model of saccade generation with respect to the role of visual attention in saccade programming.

- ◆ **Saccadic enhancement of image displacement**
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It has been frequently shown that the sensitivity to image displacement is reduced considerably during saccadic eye movements, as compared with a situation where the subject is fixating. We have demonstrated that image displacements can be perceived again as soon as a postsaccadic stimulus gap is introduced. Subjects were asked to follow target steps of 6 or 8 deg. Triggered by the saccade, a further small target shift was elicited which could occur in the same or in the opposite direction with respect to the eye movement. In the control condition, the target was visible continuously. In the 'Gap' condition, the stimulus was erased with the onset of the saccade and then reappeared, with a delay of 20 to 300 ms, at the displaced position. In the

'Background' condition, a background structure additionally was present and occasionally displaced during the saccade. In a two-alternative forced-choice task the subjects had to report the direction of the target shift. Eye movements were measured with the SRI Generation-5.5 dual Purkinje-image eyetracker.

As expected, the data from the control condition yield a low sensitivity to the intrasaccadic stimulus displacements. In the 'Gap' condition, however, discrimination performance recovers dramatically with increasing gap duration. With a gap of 200 ms, subjects are able to report correctly the direction of target displacements of as small as 0.3 deg. When intrasaccadic background displacements occur in combination with a target gap, the background shift is attributed to the target, with the result of apparent target motion. These findings suggest that a very precise extraretinal signal about gaze direction is available but is only utilized for spatial localization if consistent visual information is missing immediately after the saccade. The findings have important implications for theories of visual stability and for the nature of the information transferred across saccades.

◆ **The magical number 7 ± 7 : selection by covert visual attention**

I Kovács (Laboratory of Vision Research, Rutgers University, Piscataway, NJ 08854, USA)

The mechanisms and time course of autonomous attentional gating of visual input can be studied in a modified partial-report paradigm. As opposed to search tasks, there are multiple targets, all competing to be selected for identification. The original paradigm (Sperling, 1960 *Psychological Monographs* 74 1–29) was modified to control for foveal bias (eccentricity), signal energy (contrast and timing), spacing (crowding), and redundancy (similarity of elements that results in grouping). Patterns consisted of equally spaced elements (combinations of Gabor signals) at identical eccentricities, flashed for 50 ms. Identification performance at postcued positions was measured as a function of cue delay (0 to 500 ms), element spacing (6 to 2 times Gabor wavelength), set-size (6 to 18 elements), and set redundancy. Performance with sets of low redundancy and of constant set-size was most affected by element spacing at 0 cue delay. For constant element spacing, the size of low-redundancy sets affected performance between 180 and 250 ms. For high-redundancy sets, the compensating effect of similarity grouping occurred only above 200 ms, permitting performance of $7 + 7$.

The results are not consistent with a fatiguing pictorial representation, but are suggestive of a continuously operating selection mechanism with constraints on its spatial and temporal progression. In the time course of events, local interaction between spatial filters produces early spatial selection, and grouping along with nonneighbor feature selection reduces the number of subsets for recognition at a later time window.

◆ **VERPS for physically identical stimuli modulated by spatial attention**

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Visual-event related potentials (VERPS) to two visual randomly interspersed stimuli were recorded in two subjects from occipitoparietal-temporal regions by means of multiple scalp electrodes. The stimuli—the letters H and E—were formed from small letters E and H, respectively. The large letter occupied 12 deg (height) \times 9.65 deg (width) of visual angle while the angular size of each small letter was 0.48 deg (height) \times 0.39 deg (width). The stimulus duration was 150 ms. The subjects' task was to select and to name the large or the small letter, depending upon an instruction given to them before each stimulus presentation. The VERPs to physically identical stimuli were recorded and separated into two equal groups depending upon the instruction (large or small letter attended). VERPS averaged over these two groups of trials were compared with each other for each electrode position. Significant ($p < 0.05$) differences between the two different categories of responses were mostly observed in parietal region with latencies of 100 ms after stimulus onset. The data suggest that different assessment actions of the same visual stimulus can differentially activate the parietal cortex.

◆ **Voluntary attention switching between global and local levels**

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Our visual attentional system enables us to concentrate on the global shape of an object as well as on its details. What happens when we switch attention between such levels of an object description? A series of reaction-time experiments is described, with a paradigm that makes it possible to estimate the time necessary for a switch. Voluntary switching times are of the order

of 150–300 ms, and depend on the direction (global-to-local vs local-to-global) as well as on the size difference of the global and local stimulus components. The long times seem partly due to disengagement prior to switching. This is evidenced by much-reduced switching times when the start stimulus offsets at the moment of the switch, and when start and goal stimuli are separated by a delay.

◆ **Target and distractor similarity effects in visual search**

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In feature-integration theory (FIT) it is proposed that search should be parallel if it is based upon a single critical feature, and it should be serial, self-terminating if a conjunction of features defines a target. Effects of target and distractor similarity confuse this picture, however. In the present study, the target was always a circle or an oval, and the distractors were either (1) similar to the target and homogeneous, (2) dissimilar to the target and homogeneous, (3) similar to the target and heterogeneous, or (4) dissimilar to the target and heterogeneous. The results showed that target-search rate (estimated by the slope of the function relating mean response time to number of display items) differed among the four conditions, producing the greatest slope in condition (3), and the flattest slope in condition (2). The pattern of results cannot easily be handled by FIT, since the target differed from the distractors by a single feature (curvature), yet the slopes were generally above zero, with a negative to positive ratio greater than 2:1. The results are more readily interpretable within the framework of Duncan and Humphreys's model (1989 *Psychological Review* **96** 433–458), but more-specific models of the search process are needed to provide a complete account of the results.

SPATIAL VISION

◆ **Influence of the number of dots on the perception of interpolated Müller-Lyer patterns**

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We have tested the size of the Müller-Lyer illusion presented only by points (interpolation). The experiment consisted in simultaneous presentation of the two figures forming the Müller-Lyer pattern horizontally oriented on a computer screen. One of the two figures was fixed while the size of the other could be adjusted by the subject in order to fit with the length of the fixed figure. Each subject performed 96 of such tasks. These tasks were divided as follows: (a) one half of the tasks had the horizontal lines identified only by the two extreme points and one half by a real and complete line; (b) four different angles (30°, 50°, 70°, and 90°) were used to form the arrows for each of above configurations; (c) for each amplitude the arrows were composed, respectively, of three, five, or nine points and for each of these configurations, four different lengths of the fixed figure have been chosen. The average of the relative error [(apex-out figures – apex-in figures)/length of the fixed figure] of the four lengths was defined as mean relative error (MRE) and was used for the statistical evaluation. Seven subjects took part in the above experiment. The three-way ANOVA was performed on the MREs of all the subjects for all the above configurations. The results showed the dependence of the size of the MRE on the number of dots forming the arrow ($F_{2,167} = 20.585$; $p < 0.05$), on the configuration of the line to be fitted ($F_{1,167} = 35.171$, $p < 0.05$), and on the subjective variability ($F_{6,167} = 35.168$, $p < 0.05$). These results agreed with our previous results and with our model based on the Image-Function Theory proposed to explain the error committed on the area comparison of geometrical figures (Di Maio and Lánský, 1990 *Perceptual and Motor Skills* **71** 459–466; Mates et al, 1992 *Spatial Vision* **6** 101–116).

◆ **Subthreshold summation with illusory contours**

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Earlier experiments (Kulikowski et al, 1977 *Vision Research* **13** 1402–1624) have demonstrated that the detection threshold for a line is lowered when a subthreshold line of the same size, orientation, and contrast polarity is added to the target line. This observation is known as 'subthreshold summation', and is generally explained in terms of summative activities of line detectors in the visual cortex. If such detectors are also involved in the processing of illusory contours, as may be assumed on the basis of neurophysiological evidence (Von der Heydt et al, 1989 *Journal of Neuroscience* **9** 1731–1748), a subthreshold line should sum with an illusory line in a similar way as it does with a real one. In a two-alternative forced-choice experiment, we asked observers to detect a subthreshold line of varying contrast, added to an illusory

contour induced by elements of varying size and contrast polarity. It was verified beforehand that the line could not be detected when presented alone. The main results show that the percentage of correct detections rises from chance level (subthreshold line alone) to 95% (subthreshold line on illusory contour), depending on the contrast of the subthreshold line. These findings provide further evidence for some functional equivalence of illusory contours and real lines. Theoretical and methodological issues will be discussed in the light of theories of illusory-contour induction and classic subthreshold summation effects.

◆ **Surface interpretation affects the Craik-O'Brien-Cornsweet effect (COCE)**

A Grunewald, L Pessoa, W D Ross (Department of Cognitive and Neural Systems, Boston University, Boston, MA 02215, USA)

The basic COCE paradigm consists of a luminance cusp surrounded by two regions (A and B) of uniform luminance. Although a luminance difference exists at the cusp only, subjects report perceiving the regions as having different brightnesses. In the present study the basic paradigm was extended in order to investigate how surface interpretation influences the phenomenon. In one class of displays, both the regions, A and B, were partially blocked by vertical bars whose luminance and size could be varied. When the display configuration was indicative of regions A and B being occluded by the bars (eg bars of different luminance from the background), a matching task indicated that subjects experienced a COCE beyond the bars even though retinal contiguity was interrupted. Display configurations not consistent with occlusion (eg bars of the same luminance as the background) greatly weakened or destroyed the COCE beyond the bars. Another class of patterns employed disparity cues in order to alter the surface interpretation. Disparities were introduced in the regions in the immediate vicinity of the cusps such that a rectangular patch (comprising the cusps) was perceived in depth. When the cusp patch was seen behind or in front of the plane including regions A and B, the COCE could be greatly weakened or completely destroyed and the cusp patch could be perceived either as through a window or protruding on a platform.

The current results build on previous investigations showing that lightness is affected by perceived depth, as in Gilchrist's 'coplanar hypothesis' (1977 *Science* **195** 185-187). The present study shows that the COCE, in which brightness differences occur between regions of the same luminance, is also influenced by surface interpretation. These results suggest that theories of the COCE (eg integration or filling-in models) should incorporate three-dimensional mechanisms (Nakayama et al, 1990 *Perception* **19** 497-513).

◆ **An account of the Zöllner illusion in terms of bias in the estimated global orientation of each individual stack of oriented line segments**

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The configuration known as the Zöllner illusion consists of several parallel stacks of short segments oriented obliquely at a given angle ϕ to the direction of the stack. The absolute value of ϕ is around 30° to 60° and its sign changes from one stack to the next. There are therefore two types of stacks which are roughly mirror images of one another. There is an illusion in that stacks of opposite sign for ϕ appear to diverge where their top segments form an arrowhead. The illusion may be due to some kind of interaction between the two types of stacks, or, alternatively, it may be due to the sum of distortions occurring independently in each type of stack. In an experiment to distinguish between the two possibilities, we created a new stimulus configuration in which all stacks were of the same sign. In order to estimate the apparent global orientation of the stacks, we asked subjects to align the stacks with reference segments situated at a slight distance from them. The amplitudes of the observed biases in this 'half-Zöllner' configuration were good predictors of the amplitude of the classic Zöllner illusion, thereby giving strength to the second possibility. When the ends of the short line segments were curved so that at their endpoints they became precisely perpendicular to the axis of the stacks, the illusion was substantially reduced, but not abolished. Therefore the illusion cannot be entirely accounted for by a mechanism of alignment of illusory contours generated at these endpoints.

◆ **Intrinsic blur and the Poggendorff effect**

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The angle-induced component of the Poggendorff misalignment effect (Hotopf and Hibbert, 1989 *Quarterly Journal of Experimental Psychology* **41** 355-383) could arise because of mislocation of line terminations at oblique T-intersections (Morgan and Casco, 1990 *Proceedings of the Royal Society of London, Series B* **242** 1-10). We suggest that observers judge collinearity of

separated oblique line segments by determining the orientation of the virtual line joining their terminations and comparing this virtual orientation with the orientation of the segments themselves. The size of the misalignment effect can be predicted by convolving an image of an oblique T-junction with a difference-of-Gaussian (DOG) filter and locating the peak corresponding most closely to the intersection in the filtered image. The peak is systematically displaced in the same direction as the Poggendorff misalignment, as a function of the space constant of the DOG filter. The actual size of the Poggendorff misalignment effect was measured by the method of adjustment with Gaussian-blurred images. If the Poggendorff effect depends upon intrinsic blur, we can predict that amounts of extrinsic blur smaller than the intrinsic blur will have little effect, while with larger amounts of extrinsic blur the effect will increase linearly with blur, as does the computed displacement of the peak at the intersections. This prediction was verified experimentally, and the extent of intrinsic blur was calculated to be equivalent to Gaussian blur with a space constant of about 4 min arc. The intrinsic blur must depend upon second-order filters, because the Poggendorff effect is still seen in stimuli with balanced lines, consisting of alternating black and white segments on a mid-grey background, which would be invisible to first-order Gaussian filters with the space constants we measured.

◆ **Investigating three-dimensional-curvature contrast**

W Curran, A Johnston (Department of Psychology, University College London, London WC1E 6BT, UK)

We have investigated a previously unreported visual illusion of perceived shape—three-dimensional-curvature contrast. In this effect two spherical surface patches, defined by shading and texture cues and of identical curvature, appear dissimilar in their curvature when one patch is superimposed on a more-curved spherical surface and the other on a less-curved spherical surface. To measure the strength of this effect, subjects were given a two-alternative forced-choice curvature-discrimination task, in which they had to choose which of the two superimposed surface patches appeared the more curved. The strength of the effect increased as the curvature difference between the background surfaces increased. We found the effect persisted even when the stimuli were defined by either cue in isolation.

It is possible that the illusion could be explained solely in terms of contrast-induced changes in brightness, caused by local interaction between the test patches and their contrasting curved surrounds. We controlled for this by replacing each background surface with an array of curved patches of the same size as the test patch, with the patches in the arrays being either more curved or less curved than the test patch they surrounded. This display reverses the local brightness-induced interactions described above; thus if brightness contrast is the sole cause of the effect, one would expect the illusion to be eliminated. We found a clearly measurable, but small, effect, which suggests the illusion cannot be explained simply in terms of brightness contrast. The illusion described above, and our investigations of it, highlight the role of geometric context in the perception of three-dimensional curvature, and, as such, has some bearing on the ongoing debate of whether shape perception is a local or global operation [Marr, 1982 *Vision* (San Francisco, CA: W H Freeman); Stevens et al, 1991 *Perception* **20** 425–440]. The occurrence of curvature contrast suggests that the perception of shape from shading and/or texture cannot be a purely local operation.

INVITED LECTURE: BRIGHTNESS AND LIGHTNESS

◆ **A vector analysis approach to the perception of illumination, reflection, and depth**

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Earlier attempts have been made to apply Johansson's perceptual-vector analysis of motion to the area of colour and illumination (Bergström, 1977 *Scandinavian Journal of Psychology* **18** 180–186; Bergström et al, 1984 *Perception* **13** 129–140). In this application it was assumed that light reflected from illuminated objects is automatically analysed into common and relative components. Thus, the visual system was assumed to be able to distinguish the illumination component from reflectance components in the proximal stimulus. And it was assumed that this distinction is possible thanks to the common component characteristic of the illumination. The commonality assumption means that the visual system can discriminate between the retinal projection of an illumination border and that of a reflectance border and between the projection of a shadow and that of a darker colour because illumination has this characteristic of being a common component. It was also assumed that the modulation of illumination in space and/or time corresponds to the perceived three-dimensional layout of the scene and to motion in depth within the scene.

Empirical support for the commonality assumption is given both from the literature and from experimental studies performed in my own laboratory. It is shown that our model (the two assumptions above plus a minimum principle as to the number of perceived light sources) can be applied to a number of studies of colour (and lightness) constancy. It has been applied to Land and McCann's Mondrian demonstrations and to Gilchrist's two classes of experiments, one class giving a shift of lightness with a shift of viewing conditions, the other giving no such shift. Edges versus gradients and reflectance edges versus illumination edges are also discussed within the same theoretical frame of reference.

BRIGHTNESS AND LIGHTNESS

◆ A multiscale network model of brightness perception

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A neural theory of brightness perception is developed to account for a wide variety of difficult data. The model is in the tradition of filling-in theories and builds upon previous work by Grossberg and colleagues on explaining brightness perception through the interaction of boundary and feature signals. Model equations are presented and computer simulations illustrate its potential. Our simulations implement a number of refinements already described in the development of the form-and-color-and-depth (FACADE) theory, recently summarized by Grossberg (1994 *Perception & Psychophysics* 55 48–120), and include (a) ON and OFF channels with separate filling-in domains, (b) multiple spatial scales, (c) computations for simple and complex cells, and (d) boundary computations that engage a recurrent competitive circuit. Simulations of the present system of equations account for human perception of a wide variety of stimuli, including ones whose brightness contains smooth spatial gradients. Among the stimuli are Mach bands associated with trapezoidal luminance waves, brightness undershoots/overshoots for triangular luminance waves, qualitative difference in brightness profile for high-contrast and low-contrast missing fundamental waveforms ('veridical' cusps and square waves, respectively), brightness contrast, and nonlinear contrast effects associated with high-contrast sine waves. The model is compared with alternative approaches, particularly the MIDAAS model of Moulden and Kingdom (1992 *Vision Research* 32 1565–1582). MIDAAS accounts for the one-dimensional phenomena investigated here but does so by employing symbolic interpretation rules that, we feel, are bound to yield contradictions requiring appeal to other rules (ie a homunculus) in a two-dimensional implementation. The present formalism, on the other hand, has a natural extension to two dimensions, which has already been applied for image-processing applications.

◆ Contrast effects in paper and CRT-simulated displays

T Agostini, N Bruno (Dipartimento di Psicologia, Università di Trieste, 34123 Trieste, Italy)

We compared the size of departures from type-2 constancy in paper and CRT-simulated displays. We tested nine variants of well-known contrast illusions, including simultaneous lightness contrast, the Benary effect, and White's effect. Variants included incremental, decremental, and classic versions. Independent groups of observers were randomly assigned to one of the three following conditions. (1) Simulation—displays as well as a Munsell matching scale were simulated on a CRT monitor (approximately 2 log units). (2) Equal-luminance paper—the same configurations as used in the simulations were built by using Munsell paper. Illumination and viewing conditions were controlled in order to obtain approximately the same spatial distribution of luminance as in the simulation displays. (3) Daylight paper—the Munsell displays were tested under daylight conditions. Observers were requested to match the lightness of target surfaces in the displays by selecting the most similar patch from a series of grey squares arranged on a scale (0.5 Munsell steps). Results are relevant to the current debate on the use of CRT-simulations for studies of lightness constancy and contrast.

◆ Relationship between achromatic colour of a surface and its perceived illumination in the 'wallpaper' illusion

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It is well known that the achromatic colour of a surface (or whiteness) may be affected by its perceived illumination. These phenomenal parameters are coupled in the visual image. The question arises of whether the relationship between these parameters is influenced by the

brightness of a surface (or intensity of the light reaching the retina from the surface). By means of the 'wallpaper' illusion we quantitatively investigated the reciprocal relationship between whiteness and perceived illumination at different levels of brightness for two subjects.

The subjects looked through a grating made of white paper and fixed their eyes on a white paper screen with a black random pattern on it. The screen was placed behind the grating. The subjects observed the scene binocularly. In this situation the grating was perceived as lying in the plane of the screen and looked coloured. Changes in screen illumination induced some changes in whiteness of the apparent grating while illumination of the real grating (which is proportional to the brightness of the grating) was fixed. The subjects' task was to estimate the whiteness of the apparent grating and its perceived illumination, by the method of direct estimation. There were three experimental sessions, each for a fixed level of grating illumination (5, 10, 20 lx). In each session the screen illumination varied at eight levels in the range of 0–100 lx, 0–200 lx, 0–300 lx, respectively. Three curves of whiteness against perceived illumination were presented, each for a constant grating brightness. Our results showed that achromatic colour was related reciprocally with perceived illumination and that their product was proportional to brightness.

◆ **Spatially remote, frequency-tuned mechanisms can control apparent lightness**

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An increasing number of reported apparent-lightness phenomena require models that include spatially global processes in addition to local border-contrast mechanisms. We demonstrate here that the perceived lightness of a spatially modulated (textured) surface depends upon the relative spatial-frequency content of adjacent and remote surfaces. A display 24 deg wide was divided in half by a 20% luminance step. In the center of each half, a 4 deg test or comparison strip was always defined by a local 4% contrast increment (on the lower-luminance half) or decrement (on the higher-luminance half), yielding six distinct regions across the display. The observer's task was to adjust the mean luminance of the comparison to match that of the test. When regions are internally unmodulated, it is well known that the increment appears even lighter than the physically more luminant decrement, presumably owing to local border-contrast effects. We sinusoidally modulated the luminance of each region with vertical gratings of variable spatial frequency (ranging from 0.5 to 6 cycles deg⁻¹ in half-octave steps; contrasts set to 0.5 log units above threshold), according to two spatial patterns. When frequency was identical across the three regions in each half of the display, but different across the two halves, apparent lightness was as expected from local contrast effects. However, when test and comparison fields shared the same frequency, and the remaining background fields shared a different frequency, then matches were nearly veridical with physical luminance. Matches became increasingly influenced by local contrast effects as test and comparison frequencies diverged. The results suggest that apparent lightness is in part determined by frequency-selective mechanisms capable of pooling responses across remote spatial locations.

◆ **The albedo hypothesis revisited**

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It was found in the preliminary experiment (Logvinenko and Menshikova, 1993 *Perception* 22 Supplement, 54) that, although achromatic colour varied approximately in inverse proportion to perceived illumination under pseudoscopic inversion of an apparent relief of a surface, the albedo hypothesis as it was originally formulated by Koffka ($\bar{I}\bar{G} = kl$, where \bar{I} is an apparent illumination of the surface, \bar{G} is greyiness of a surface colour, and l is a luminance of light reflecting from the surface) did not hold true. However, as further analysis shows, the experiment data are in line with the following modification of the albedo hypothesis:

$$\bar{I}\bar{G} = \phi(l). \quad (1)$$

The shape of the function ϕ , as revealed in our experiments, is similar to that of a psychophysical 'brightness–luminance' function. In other words, the perceived illumination and neutral colour covary directly proportionally to brightness rather than, as it has been widely believed so far, to retinal illumination, provided one of the two terms in equation (1) is fixed. So, a new version of the albedo hypothesis may be written as

$$\bar{I}\bar{G} = kb, \quad (2)$$

where b is brightness of light entering the eye.

◆ **Simultaneous contrast and color constancy: different, similar, or identical mechanisms**

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Simultaneous contrast, simply stated, is that color sensations show a dependence on the stimuli surrounding a test area. Color constancy, simply stated, is that color sensations are roughly constant, despite very large changes in illumination. Historically, they are associated with different experiments, hence they are usually assigned to different visual mechanisms. Simultaneous-contrast experiments demonstrate that the appearance of an area depends on the size, the amount of enclosure, and the separation of certain so-called inducing stimuli in the surround. In other words, simultaneous contrast is controlled by both the stimuli and the spatial distribution of those stimuli in the surround. Color-constancy experiments show that humans normalize to the maxima in the field of view. Simultaneous-contrast and color-constancy experiments can both be understood by using the same framework of independent normalization of long-wave, middle-wave, and short-wave systems, each of which has a dependence on the spatial location of the maxima.

HIGH-LEVEL VISION

◆ **Object-based perception of ego-motion**

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Current research on egomotion is almost exclusively based on the assumption that optic flow fields feed directly into a putative 'heading module'. We believe this assumption is misguided. As an alternative we propose that the locomoting observer first constructs a simple scene model; perceived heading will then be based on the observer's perceived motion with respect to objects in the scene. We do not discount the importance of image motion, but maintain that it plays a role only via objects. We explored the implications of this hypothesis through two experiments.

In the first experiment we compared perceived heading in a structured scene with that in an unstructured scene. The structured scene consisted of a simulated room (7 m long, 4 m wide, and 2.5 m high), which contained various objects with colored surfaces such as chairs and tables. The unstructured scene consisted of 150 large dots whose depth varied randomly between 0 and 7 m. The observer translated 1 m s^{-1} . Simulated eye rotations varied between 3 and 8 deg s^{-1} , and heading angles between 10 and 30 deg. The horizontal field of view was 90 deg. Perceived heading was more accurate in structured than in unstructured scenes, even though the optic-flow fields associated with the latter were more salient. In the second experiment we studied perceived heading in scenes consisting of a single house-like object plus a horizon. The object was a concave or convex dihedral with 'windows' painted on the two planar surfaces. By making the object's outline either convex or concave, its perceived shape could be manipulated (a kind of Mach-Ames illusion). Perceived heading with respect to the object varied with perceived shape rather than image motion. Both experiments show that perceived heading depends more on the salience of the perceived scene than the salience of the optic-flow field.

◆ **Probing depth and attitude in pictorial space: a comparison of methods**

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We used different local probes to study the 'pictorial relief' (a surface in 'pictorial three-dimensional space') evoked by (flat) pictures. For each probing method it is possible to derive a pictorial relief map from the psychophysical data. Comparison of the results for the different methods gives us insight into the nature of pictorial-depth perception. Stimuli are photographs of real objects. Physical conditions in the original scene, such as the lighting, the geometry, and the perspective, were controlled by the experimenter. The subjects judged depth and attitude (slant and tilt) of the pictorial relief in the photographs by using the following methods: (1) probing depth order of nearby points on the picture surface by a method of direct comparison; (2) probing depth order of arbitrarily separated points on the picture surface by a method of direct comparison; (3) probing surface attitudes—slant and tilt settings are made by adjusting an elliptical loop superimposed on the picture surface so that it appears as a circle painted on the pictorial surface; (4) probing surface attitude by adjusting an arrow superimposed on the picture surface so that it appears to point in the direction of the depth gradient;

and (5) probing surface attitude by adjusting a line segment superimposed on the picture surface so that it appears to coincide with the direction of equal depth.

For all these probes we reconstructed the pictorial relief, that is, the psychophysical 'response surface' in three-dimensional pictorial space. The concordance and discordance of these surfaces is reported and psychometric curves and Spearman rank correlations of depths are presented. At this stage it is concluded that pictorial relief is naturally represented as a field of contact elements (slant and tilt), and not as a direct depth map.

◆ **Binocular flow improves the robustness of human heading perception**

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The retinal flow during normal locomotion contains components due to rotation and translation of the observer. The translatory part of the flow pattern is informative of heading, because it radiates outward from the direction of heading. However, it is not directly accessible from the retinal flow, because of the rotational component. Nevertheless, humans can perceive their direction of heading from the compound retinal flow without need for extraretinal signals that indicate the rotation.

For simulated motion across the ground plane, heading perception is more noise tolerant in humans than in the optimal observer, which uses optic flow only. Humans use more information than contained in the optic flow. The excess performance is caused by the use of static monocular depth cues. These cues impose a depth order on the flow, which makes possible the selective processing of the most-distant flow vectors. Based on these vectors, the estimate of the ego-rotation is the most reliable, because the translatory component of the flow is inversely proportional to the distance. When monocular static depth cues are absent, as for simulation of motion through a random cloud of dots, human performance drops below that of the optimal observer. When binocular flow patterns are presented, robustness is identical for motion through the cloud and for motion across the plane.

◆ **Visual capture and transparency in blocked images**

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Coarse quantised or blocked images are difficult to recognise, despite the fact that the blocking process preserves sufficient low-frequency harmonics for easy image recognition. We have quantified the magnitude of the blocking effect by measuring minimum signal-to-noise ratios necessary for recognition of blocked and unblocked letters. Quantisation at 8 blocks per image reduces sensitivity by more than a factor of 10. However, if the phase of the spurious frequencies is shifted by a constant amount (not affecting their contrast), letter recognition improves. For a shift of 180° (which simply inverts the contrast of the spurious frequencies), the letters were seen in transparency through the blocks, and sensitivity was the same as for the unblocked image. The results are difficult to reconcile with the original critical-band-masking theory, but can be readily explained by the local-energy model of Morrone and Burr (1988 *Proceedings of the Royal Society of London, Series B* **235** 221–245). When the harmonics are in phase with the low-frequency signals, at all spatial scales the peaks in local energy (which are defined by phase congruence of harmonic components) occur at the borders of the blocks, segmenting the visual scene into blocks. When the spurious harmonics are out of phase, phase coherence across scales is broken, so the letters and spurious frequencies form independent peaks in local energy, perceived as separate transparent images.

◆ **A scale-space measure of image complexity**

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The perception of complexity of a visual scene is determined by the structure of the environment as well as the abilities of the observer. As a paradigmatic example consider two observers, one with normal vision and one myopic, both looking at the same scene. They will perceive the scene differently because the myopic simply can not see all the details. The complexity judgment of the myope will therefore differ from that of the observer with normal vision. Although this fact is crucial it has rarely been incorporated in measures of complexity used in experimental psychology.

We simplify the situation by reducing the environment to a two-dimensional image and the observer to the 'front-end' or 'bottom-up' part of the visual system. The image is described by the irradiance $I(x, y)$ whereas the front end is described by the scale-space model (Koenderink, 1984 *Biological Cybernetics* **50** 363–370). The most important characteristics of the front end is

its scale invariance; there is no a priori preferred scale. We characterise the situation by the dictum that aspects of the structure of the image that are not encoded by the front end do not exist for the observer. A mathematical measure $\Theta(I, V)$ is derived that assigns a value to a given image I and to a given front end characterised by a set of relevant parameters V as the size of the visual field and the range in the scale domain. The derivation is based on the scale-space model and the Shannon-entropy [Shannon, 1948 *Bell Syst. Techn. J.* **27** 379–423, 623–656]. The measure $\Theta(I, V)$ must be interpreted as an information load that indicates how much information is available in a particular situation. We report the results of psychophysical experiments concerning complexity judgments by human observers.

◆ **Image-representation chaining and scene perceiving**

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Our work is aimed at describing the influence of perception in the organisation of the image-representation schemes for a scene-recognition system. Image transformations are common at the various levels of a computer-vision system. Transformations occur during the early processing, the segmentation, the low-level perceptual-organisation detection, and the high-level interpretation. In general we can describe an image transformation with a chain from a starting image representation or 'initial status' to an ending image representation or 'final status' through a series of state transitions and intermediate representations. A state transition results in data-structure transformations (array to array, array to quadtree, polygons to polygons, etc), and it can be viewed as a nondeterministic process involving knowledge, both domain independent and domain dependent. When transition criteria are derived from candidate object-models, extracted from a knowledge base, scene recognition, which can be considered as a 'final-status' example, becomes a process of evidence accumulation focused by expectations.

In our approach to scene recognition, we adopt an automatic focusing of attention and spatial and temporal relations to reduce the search space. Anyway, a fundamental role is played by an intentional behaviour, which we call 'attraction', of the transformed visual data. That is, data are forced to be the object model until strong evidence of the contrary is achieved. We can also relate the perceptual-organisation principles [Lowe, 1985 *Perceptual Organization and Visual Recognition* (Dordrecht: Kluwer)] to 'attraction'. The transition processes result from a complex transformation driven by perceptual data (eg a red-coloured blob, two parallel lines) or by models both domain-dependent (eg car) and domain-independent (eg polygonal). The reading (number, type, quality, etc) of the perceptual data influences the nondeterministic image-representation chaining.

SHAPE, TEXTURE, AND DEPTH

◆ **Extraction of three-dimensional shape from optic flow**

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We show how a complete set of measures of three-dimensional shape can be derived directly from the velocity field generated by a rigid curved surface patch under perspective projection. We use invariance under rotation of the image plane [the Lie group $SO(2)$] to decompose the second-order velocity field into differential invariants. These invariants are the gradients of divergence and rotation (Koenderink and van Doorn, 1975 *Optica Acta* **22** 773–791) and the double deformation. From combinations of these invariants we construct approximations to Koenderink's shape index and curvedness (Koenderink and van Doorn, 1992 *Image and Vision Computing* **10** 557–565) and to the principal directions. We show theoretically that the effect of these approximations is small when the radius of curvature of the surface is large compared with the viewing distance.

We have tested experimentally one of the predictions of the theory by adding noise to the velocity field generated by a rigid curved surface patch rotating in depth. The noise was temporally white and spatially structured as one of the second-order differential invariants and was either parallel or perpendicular to the direction of movement. The subjects were shown a pair of rotating noise-corrupted surfaces and the task was a two-alternative forced-choice discrimination between the planar and nonplanar patch. The results confirmed qualitatively the predictions of the theory. For instance, double-deformation noise orthogonal to the direction of movement had relatively little influence on the discrimination threshold whereas this noise parallel to the movement direction induced an increase in the threshold especially for a hyperbolic patch.

◆ Strong interaction of disparity and shading cues

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Experiments were designed to test whether the visual system uses shading cues to reduce the aperture of regions in each eye for possible feature matching. The facilitation effect of shading cues on the time of stereo-shape perception was used to study the interaction of disparity and shading cues. Test images were random-dot stereograms (RDSs) of quadratic surfaces (elliptic and cylindrical) displayed as red/blue anaglyphs. Shading cues were introduced into the RDSs by changing the brightness of dots. The brightness distribution was computed for Lambertian surfaces with the same (consonant cues) or another (contradictory cues) shape as compared with that depicted by the disparity cue. The course of each trial was as follows: a depth fixation, test-image presentation for a random time, and the noisy-depth-mask presentation. The observers' task was to indicate whether they perceived a convex or concave surface shape. An unwanted influence of the time needed to make a vergence eye movement on the perception-time value was stabilised by fixation of observers' gaze at some depth before the test presentation. A significant (Mann-Whitney two-sample statistic U) facilitation effect was found for consonant disparity and shading cues of an egg-like surface shape. An identical effect was found in cases both of collinear and of mutually orthogonal orientation of the disparity and shading gradients for a cylinder-like surface shape. The shading cues were found to facilitate the shape perception of the concave and convex RDS surfaces, though shading cues alone were perceived ambiguously. The data demonstrate a strong interaction of disparity and shading cues in the visual system [Clark and Yuille, 1990 *Data Fusion for Sensory Information Processing System* (Dordrecht: Kluwer); Buelthoff and Yuille, 1991 *Comments on Theoretical Biology* 2 283–314].

◆ What the eyes see and you don't in random-dot stereograms

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Often it takes a long time to recognize forms which are presented in random-dot stereograms (RDSs). We found that eyes detect attributes like positions of edges and correct vergence levels long before recognition occurs. This detection occurs even when the forms are not recognized at all. Is this a hint of separate processing?

With a binocular eye-tracker (AMTech) we recorded horizontal and vertical eye positions while the subjects were viewing RDSs. Vergence was calculated from the horizontal position of both eyes. The subjects had a switch in hand to indicate when the forms were recognized. Five different forms were used as stimuli; each was projected in two colors onto the same location on a semitranslucent screen. Nine subjects viewed the RDS through the respective color filters in front of each eye. Attributes were considered 'detected' by the eyes when the eyes gazed on an edge (within 1 deg) and/or had 'correct' vergence response (sustained, and according to the appropriate disparities in the RDS). On average, detection of attributes by the eyes takes one third of the duration that recognition does (3.6 s). The fraction of time it takes for detection of attributes by the eyes becomes smaller when the duration for recognition gets longer. In the cases where the forms were not recognized during the recording (13 s or 15 s), the detection by the eyes was made within 2 s. In some of these cases the images were blurred to prevent recognition. Detailed consideration of the results suggests two separate and interactive sub-systems and pathways, where both process stereo and edges—an autonomic precognitive one, which controls eye movements, and one for recognition. The precognitive subsystem processes mainly low spatial frequencies. By analogy with blindsight, the precognitive subsystem is composed of the subcortical visual nuclei.

◆ Are eye movements necessary in order to use vertical disparities?

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It has been claimed that when the fall-off in disparity sensitivity with retinal eccentricity is taken into account, the human visual system would not be able to exploit vertical disparities unless observers direct their gaze to the eccentric regions of stereoscopic images (van de Grind, 1993 NATO Advanced Research Workshop, Toronto, June). The claim was based on modelling the fall-off in sensitivity with eccentricity rather than from empirical results. Two different tasks were used to determine the effects of vertical disparities as a function of (i) fixation versus free viewing and (ii) display size. In the first task, observers discriminated the perceived depth of corrugated surfaces by using a forced-choice procedure. In the second task, observers discriminated the direction of perceived curvature (along a horizontal meridian) of surfaces close to the fronto-parallel. For both tasks, the overall size of the stereoscopic images was either 10, 20, 40,

or 80 deg in diameter. Depth discrimination improved with increasing display size up to the largest value, even when fixation was held in the centre of the display. Direction of curvature discrimination from the fronto-parallel similarly improved with display size.

These results show that the human visual system is able to use the vertical disparities generated by three-dimensional surfaces even when retinal areas as eccentric as 20–40 deg from the fovea are stimulated. Performance was only slightly better when observers were allowed to scan the display field. As a follow-up, the second experiment was repeated but with manipulations in the horizontal rather than the vertical disparity field. With 80 deg displays, sensitivity to vertical disparity changes was only slightly poorer than to horizontal disparity changes, but with small, 10 deg displays, sensitivity to vertical disparity changes was at least four times poorer. Our results also show that whilst vertical disparities only affect the amount of perceived depth in large displays, they affect fronto-parallel surface judgments with displays as small as 3 deg.

◆ Poggendorff illusion and depth cues with binocular disparity

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The relationship between the Poggendorff illusion (line-discrepancy effect) and depth cues with binocular disparity has been investigated in connection with new types of three-dimensional (3-D) illusion (Idesawa, 1991 *Japanese Journal of Applied Physics* **30-4B**, L751, **30-7B**, L1289). The Poggendorff illusion can also be seen when both of the lines and the rectangular inducing element are displayed as illusory surfaces with pacmen. This illusion has been investigated by changing the depth difference between the line element and the inducing element for both the real and the illusory figure. The line-discrepancy effect varies when the depth difference between line segment and inducing element is changed.

The Poggendorff illusion could be observed when the line element was placed at an equal depth to or beyond the rectangular inducing element. Surprisingly, the line-discrepancy effect vanished almost completely when the line segment was placed in front of the inducing element. However, the effect was clearly recognized with monocular viewing. These newly found phenomena suggest that the Poggendorff illusion may originate in the process in the human visual system for perceiving 3-D space. In addition, even when the local intersecting angle between the line element and the boundary of the inducing element was kept at a right angle, the line-discrepancy effect could still be observed, though it became a little bit smaller. This fact tells us that the Poggendorff illusion is produced not only by the local features but also by the global features of the inducing element. It may have a very close relationship with occlusion or covering, in the process in the human visual system for perceiving 3-D space. These newly found phenomena have a close relationship to the visual perception of 3-D space and can offer a clue to revealing the mechanism underlying the ability of the human visual system to perceive 3-D space.

EARLY VISUAL PROCESSING II

◆ Stochastic interactions among pattern-specific detectors

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In most current models of pattern detection the existence is assumed of a fixed set of channels in the human visual system, and detection of a stimulus pattern is assumed to be the result of probability summation among these channels. However, the hypothesis of probability summation among any sort of channels may be rejected if (i) linear contrast-interrelationship functions (CIFs) derived in superposition experiments with stimulus patterns of the form $\phi(m)s_1 + ms_2$ [where s_1 and s_2 are patterns, $\phi(m)$ and m are contrasts] and (ii) parallel (on log-contrast scales) psychometric functions, corresponding to different parameters of stimulus patterns, are found (Mortensen, 1988 *Biological Cybernetics* **59** 137–147). We present data from superposition experiments satisfying these criteria for certain ranges of m and $\phi(m)$. Detailed analysis of the data provides strong support for the hypothesis of detection by matched filters (Hauske et al, 1976 *Biological Cybernetics* **22** 181–188), in particular by a filter F_1 matched to the stimulus pattern s_1 , and by a filter F_2 matched to the background pattern s_2 . These filters are considered to develop as a result of certain self-organisational processes in the visual system that will be discussed in detail elsewhere. For $\phi(m)/m > K_1$ (a certain constant) the pattern is detected by F_1 , for $\phi(m)/m < K_2$ (another constant) the pattern is detected by F_2 , and for $K_1 < \phi(m)/m < K_2$ the pattern is detected by probability summation among F_1 and F_2 . The model predicts the CIFs to form lozenges whose shapes depend upon the spatial frequency of the background

pattern and upon a parameter, characterising the psychometric functions, which is invariant with regard to different stimulus patterns. The relationship of the model to other models, eg the Burr-Morrone model of detection according to local energy is briefly discussed.

◆ **A neural model of the visual temporal response function**

A I Cogan, L L Kontsevich (Smith-Kettlewell Eye Research Institute, San Francisco, CA 94115, USA)

We regard the biphasic impulse response function (IRF) proposed by Watson (1982 *Vision Research* **22** 1335) as a fast response originating in the excitatory center of a receptive field and modified (inhibited) after a certain delay by the response from the slower, antagonistic surround. Watson's model accounts well for two-pulse interactions, but it fails to predict the characteristic dip in the relationship between sensitivity and flash duration, while the triphasic IRF proposed by Roufs and Blommaert (1981 *Vision Research* **21** 1203) does predict the dip. It is well known that the center-surround antagonism is manifested in the receptive fields both of retinal ganglion cells and of simple cortical cells. We assumed that these two sites completely define the shape of the IRF and act together as a second-derivative operator providing the triphasic impulse response. Whether or not the response is balanced depends both on luminance and on spatial frequency, which affect the responses of both the ganglion cell and the cortical cell. Departure from perfect balance leads to a systematic reduction in the slope of the temporal modulation transfer function (MTF) in the low-frequency range. The discrepancy between large-field and small-field results can be easily explained in terms of our model. We applied the model to the data presented by Roufs and collaborators and obtained a good fit to their IRF and temporal MTF data. We argue that the apparent sustained and transient components of the temporal response indicate an imbalance of the center-surround interaction, rather than the existence of two separate mechanisms.

◆ **An analysis of psychophysical and physiological adaptation with a dynamic photoreceptor model**

P Gaudiano, N A Mejia-Monasterio (Department of Cognitive and Neural Systems, Boston University, Boston, MA 02215, USA)

Biological visual systems exhibit a remarkable ability to adapt in response to changes in ambient illumination levels. Psychophysically, adaptation can be observed by monitoring sensitivity to flashes or flickering stimuli as background intensity is varied. Physiologically, adaptation is required in order for visual neurons with a narrow operating range to remain sensitive over a broad range of inputs. While several researchers have studied the link between the physiology and psychophysics of adaptation, there is no single model that can explain this link analytically. A recent model by Graham and Hood (1992 *Vision Research* **32** 1373-1393) combines static and dynamic models of adaptation. This model provides qualitative fits of both flash and flicker sensitivity, but it does not provide a clear indication of the physiological basis for adaptation. We have shown (Gaudiano, 1993 *Perception* **22** Supplement, 142) that Carpenter and Grossberg's (1981 *Journal of Theoretical Neurobiology* **1** 1-42) dynamic nonlinear photoreceptor model based on known elements of the phototransduction process in vertebrate receptors is able to capture several types of psychophysical data, including all the results by Graham and Hood (1992). In this presentation we focus on the analytical aspects of this photoreceptor model. Specifically, we show that a general class of time-varying differential equations used in our model subsumes other well-known equations that have been used to describe various aspects of physiological and psychophysical adaptation, including static nonlinear equations (eg the Naka-Rushton equation) and linear or quasi-linear differential equations (eg linear equations with modifiable time constants). We argue that time-varying differential equations are convenient for modeling visual processing because they provide greater flexibility than linear time-invariant differential equations, without adding significant analytical complexity. By means of these equations our model is able to capture functional aspects of the neural and biochemical processes of phototransduction without introducing unnecessary detail.

◆ **A simulation program for anatomically based neural network modelling of primate visual system**

Q Wu, J S Lund, J B Levitt (Department of Visual Science, Institute of Ophthalmology, London EC1V 9EL, UK)

Although neural network modelling is gaining wide attention in vision research, there have been very few models of cortical visual information which conform to actual neuroanatomical and physiological constraints. We have developed a neural network simulation program on the Macintosh computer for anatomically based modelling of the primate visual system. The program is furnished with a strong visual interface so that the modeller can interactively specify the architecture of the neural network to resemble the real anatomical circuitry to be modelled.

Having constructed the network, the modeller can then feed it with various types of stimuli and examine simulation results such as unit firing rates, receptive-field organisation, and contrast sensitivity. Moreover, the program provides a framework to build-in transfer functions for some elementary types of neurons found in primate visual system, such as rods and cones, ganglion cells, spiny stellate neurons, interneurons, and pyramidal neurons. We have used the program to build a model for the parvocellular and magnocellular (P and M) pathways from lateral geniculate nucleus (LGN) to the thalamic recipient layer 4C in primary visual cortex of macaques. Physiological data indicate that neurons in layer 4C show a gradient of receptive-field sizes and contrast sensitivity from top to bottom of the layer. Our simulation suggests that this gradient may result from a linear combination of synaptic strengths of LGN P and M inputs on spiny stellate cells in layer 4C.

◆ **A neurobiologically and psychophysically consistent model of the vertebrate retina**

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The processing performed by the vertebrate retina begins to be well understood although its influence on subsequent stages still remains unclear. In order to clarify the retinal function in visual perception, we propose one approach in which we attempt to infer functional properties from the neural architecture of the retina. Our retinal model is simple enough to be analysed with the classical signal-processing tools, and realistic enough to have a functional relevance. This model consists of two functional layers, the outer plexiform layer (OPL) and the inner plexiform layer (IPL). Each of them is made up of several neural layers. Each neural layer is modelled by a resistive grid with different spatial characteristics reflecting the coupling between neighbouring neurons of the same layer. Each neuron is finally modelled by a leaky integrator.

The antagonistic interaction between the photoreceptors and horizontal-cells layers (in OPL) gives rise to an inseparable spatiotemporal bandpass filter. So, in the signal domain (eg for image sequences) this filter realises a contrast and motion enhancement. This output of the OPL filter conveys the X-type retinal response into the IPL through the bipolar-cell layer. The processing performed by the amacrine and ganglion-cell layers (in IPL) was theoretically deduced and correlated with the known data concerning its function in motion analysis (detection of motion and directional selectivity). The specific IPL processing provides the Y-type and W(DS)-type retinal responses. To complete this retinal model, chromatic and adaptive features have also been added at the level of the photoreceptor.

Moreover, the model has also led to a realistic simulation tool for early visual processing including that of space, time, and colour data. Since this structural model has shown properties similar to those provided by neurophysiology and psychophysics, it allows us to expect a reduction in the gap between neurobiological and psychophysical data. Therefore, this model (and its simulation tool) can provide a realistic output signal of the retina, and it can be used as the input signal of further structures.

◆ **A neurophysiological model of the Oppel-Kundt illusion**

A Bulatov, A Bertulis (Kaunas Medical Academy, Mickevichaus 9, Kaunas 3000, Lithuania)

The phenomena of geometrical illusions suggest that the metric in the perceptual field is different from the metric in the physical stimulus. In most cases investigators are prone to consider illusions as psychological occurrences. We have made an attempt to approach the problem from the physiological side. There is evidence that assemblies of simple cortical cells form the bandpass filters, which reduce sensory information passing from retina to higher cortical levels.

Neurophysiological data suggest that simple cortical cells may be described by products of a Gaussian envelope and periodic functions (Gabor element). Frequencies of periodic components produce series with stated intervals of 0.5 octave (Glezer et al, 1990 *Perception* **19** 344), the highest frequency being about 25 cycles deg^{-1} . The bandwidth of simple cells equals on average 1.4 octave (De Valois et al, 1982 *Vision Research* **22** 545-559). We suppose that simple cells located in close vicinity within the same cortical layer have overlapping receptive fields of the same orientation and size, and their weighting functions are conjugated by Gilbert transformation. Owing to conjugation, the output signal of a complex unit is independent of the phase of the periodic component of the Gabor element. The complex units are optimised for extraction of the envelope of signal and weighting-function convolution. Because of the operation of these units in the primary visual cortex, certain regions of spatial frequencies are picked up from the global spectrum of the signal. According to neurophysiological findings, distribution of receptive fields of different size in the retina may be determined by a law similar

to the chi-square. The filtering model proposed has been tested by Oppel-Kundt figures. Both qualitative and quantitative agreement between psychophysical measurement of the strength value of the illusion and predictions of our model was obtained. Our model also offers a unified explanation of other geometrical illusions.

INVITED LECTURE: MOTION PERCEPTION

◆ Spatiotemporal filtering and feature-matching in motion perception

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Vision uses two broadly different strategies in the representation of motion from image sequences: direction-selective filtering and feature or 'token' matching across space-time. I review recent evidence that confirms this broad distinction, and reveals more about the spatio-temporal and binocular properties of the two processes. I also discuss the relation between direction-selectivity and spatiotemporal gradient models, in which velocity can be extracted from spatial and temporal derivatives without the explicit use of directional filters.

Experiments on contrast detection at threshold imply that moving and flickering gratings, and even single flashes of a grating, are detected by direction-selective filters. In two-flash experiments the variation of grating threshold with spatial phase offset and time delay between the flashes is fitted well by the predictions of the Adelson-Bergen motion-energy model. Above threshold, experiments on perceived direction for gratings that are both displaced and contrast modulated over time suggest a modification to the final stages of the energy model. If we denote the two directional energy-response values as L and R , then instead of computing direction from motion opponency $(L - R)$ our experiments suggest that direction may be obtained from 'motion contrast' $(L - R)/(L + R)$.

We explored the spatial-filter properties of motion perception with a variety of spatio-temporal sequences, in which local phase shifted to the left and to the right in alternate strips or columns of the pattern. We assume that perceived motion breaks down when two strips containing opposite motion occupy the receptive field of the mechanism. On this basis the receptive fields for motion are quite small, and spatially very broad band, confirming by a very different technique the conclusions of Anderson and Burr (1991 *Journal of the Optical Society of America A* **8** 1330-1339). For example, at 1 cycles deg^{-1} the standard deviation of the receptive-field envelope is only 6 min. Such broadband filters offer a direct low-level basis for the coherent motion seen in moving plaids.

MOTION PERCEPTION

◆ Relative visual motion and motion aftereffects

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The motion aftereffect (MAE) can be induced after linear or rotary motion in the frontoparallel plane. Relative visual displacements during linear motion can be controlled in a manner not possible for rotary motion. We have previously reported that linear MAEs require relative visual displacement (Swanston and Wade, 1992 *Perception* **21** 569-582): when motion is induced in a central, stationary grating by motion of gratings above and below it, a large MAE is measurable for the central grating. In experiment 1 the durations of such linear MAEs following a range of monocular and binocular adaptation and test conditions were found to have similar relations to one another as those reported previously after rotation. In experiment 2 the importance of excluding all background illumination was demonstrated. The dependence of the MAE on the orientations and separations of the central and surround gratings was examined in experiment 3; neither factor influenced the duration of MAEs. It is suggested that induced motion is a consequence of stimulating detectors for relative visual motion and their adaptation results in MAEs.

◆ Contrast response of elementary motion encoders

J Allik, A Pulver (Department of Psychology, University of Tartu, Tartu EE-2400, Estonia)

The observer's ability to identify direction of apparent motion in a sequence of two short light pulses of different amplitudes at separate spatial locations was studied. The product of pulse amplitudes is a very poor predictor of such performance when one of the two signals is much higher in amplitude than the other; above a certain amplitude, the probability of correct identification becomes virtually independent of the amplitude of the larger pulse. There was no noticeable difference in performance between sequences of low-high and high-low contrast.

Both the direction-identification and the simple contrast-detection probabilities can be represented by the same psychometric function of the luminance increment ΔL , provided that ΔL is normalised by the n th power of the background luminance level. These results suggest that the general Reichardt-type scheme of movement encoding should be modified in the manner proposed for the fly visual system (Egelhaaf and Borst, 1985 *Journal of the Optical Society of America A* **6** 116): (1) the mean luminance is subtracted from the input signal before it is subjected to a nonlinear compression; and (2) saturation characteristics are inserted into both branches of the two mirror-symmetric motion-detection subunits before the multiplication of the input signals is performed. A probabilistic interpretation of this modified Reichardt scheme is discussed. According to this interpretation, the elementary movement encoder is a threshold device which can be in two possible states, nonactivated (Boolean 0) or activated (Boolean 1), depending on the probability of the conjoint detection of two disparate visual events. Thus, motion perception can be understood as a special case of contrast detection, that is, the conjoint detection of at least two visual events in specified spatiotemporal positions.

◆ **Integration of first-order and second-order motion signals in the human visual system**

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Previous research in motion perception indicates that first-order (luminance-defined) stimuli and second-order (texture-defined) stimuli are processed by different visual mechanisms (eg Mather and West, 1993 *Vision Research* **33** 1109–1112). An experiment was conducted to investigate how responses from the two putative mechanisms are integrated. Direction-discrimination performance was measured for two types of two-frame random-dot kinematogram: (i) single order, in which all dots were first order (dark against a grey background), or all were second order (textured against a grey background); (ii) mixed order, in which some dots were first order, and some second order. Performance was assessed at a number of different dot densities, ranging from 5% to 40% [previous research has established that discrimination performance improves as density falls (eg Morgan and Fahle, 1992 *Proceedings of the Royal Society of London, Series B* **248** 189–198)].

If signals generated by first-order dots are not integrated with signals generated by second-order dots before a decision is made about global direction, then results in mixed-order stimuli should match results in single-order stimuli at lower density. If signals from first-order dots are integrated with signals from second-order dots, then results in mixed-order stimuli should match results in single-order stimuli at the same density. Results support the second prediction. In further experiments we examined the nature of the integration between first-order and second-order dots.

◆ **Motion extrapolation and the Aubert–Fleischl phenomenon**

W H Ehrenstein (Institut für Arbeitsphysiologie, Ardeystrasse 67, 44139 Dortmund, Germany)

A small light (diameter 0.2 deg) moved from left to right over 12 deg at 6 deg s⁻¹ and then disappeared. Subjects had to press a key at the moment when the occluded (extrapolated) target motion would have reached a predetermined position (reference). The reference was one of five pairs of LEDs located above and below the horizontal trajectory, marking extrapolation distances of 2, 4, 6, 8, or 10 deg. In one session fixation was at the centre of the target LED pair from motion onset until the key press (afferent motion), in the other session subjects had to pursue the moving target with their eyes until it disappeared and then direct their gaze to the given LED position (efferent motion).

Linear regression analysis of the mean extrapolation times (from motion offset to key press) showed a high correlation ($r = 0.999$) for afferent and efferent conditions with extrapolation distance, which is consistent with a linear model of motion extrapolation (Yakimoff et al 1993 *Human Factors* **35** 501–510). However, the slopes of the regression lines differed for afferent (192 ms deg⁻¹) and efferent (238 ms deg⁻¹) conditions ($p < 0.03$), indicating a slower extrapolation velocity for efferent motion (4.2 deg s⁻¹) than for afferent (5.2 deg s⁻¹). This reduction (19%) in extrapolation velocity might be closely related to the Aubert–Fleischl phenomenon, a reduction in perceived velocity in which stimulus velocity during ocular pursuit is underestimated as compared with its perception during static fixation (Dichgans et al, 1975 *Experimental Brain Research* **23** 529–533). The possibility of using an extrapolation task as an alternative method to quantify the Aubert–Fleischl and related phenomena such as the ‘acceleration illusion’ (Wertheim and Van Gelder, 1990 *Perception* **19** 471–482) is discussed.

◆ Discrimination of dynamic orientation changes

M J Wright, K N Gurney (Department of Human Sciences, Brunel University, Uxbridge, Middx UB8 3PH, UK)

Discrimination thresholds for orientation of stationary contours are acute, with differences in the range 0.6° – 1.5° commonly found. We have shown that there is an increased sensitivity, as low as 0.35° , to dynamic orientation changes. Such a sensitivity would potentially be useful for the analysis of optic flow (Koenderink, 1986 *Vision Research* **26** 161–180). Thresholds were measured for discrimination of direction of a step angular rotation of gratings and plaids, by means of a method of constant stimuli. The addition of simultaneous phase displacements (translation) up to 180° had little effect on rotation thresholds even when these were an order of magnitude larger than the displacements due to rotation. It would appear that the detection of rotation is independent of sensitivity to translating motion. The dynamic sensitivity to rotation also appears to be independent of static orientation discrimination. Angular rotation thresholds increased with interstimulus interval (ISI) but the curve fell into two distinct linear segments. Discrimination is mediated at short ISIs (180 ms or less) by a dynamic mechanism, and is accompanied by a clear percept of motion along a curved path, but at ISIs up to 10 s it must rely on a purely spatial strategy (comparing static component orientation with memory). However, when spatially uncorrelated compound gratings were used in the two stimulus frames, there was no short-range portion of the curve, suggesting that the dynamic sensitivity to orientation change depends on correspondence of luminance contrast, like the short-range motion process. When the spatial frequency of the grating in the two frames differed, sensitivity showed sharp spatial-frequency tuning even when phase was randomised. The relationship of these results to hypothesised mechanisms for the detection of rotation ('curl') is discussed.

◆ Paradoxical motion in stationary patterns

N Bruno, P Bressan† (Dipartimento di Psicologia, Università di Trieste, 34123 Trieste, Italy; †Dipartimento di Psicologia Generale, Università di Padova, 35139 Padova, Italy)

Recently, Spillman et al (1993 *Investigative Ophthalmology and Visual Science* **34** 1031) investigated an intriguing effect of paradoxical motion (PM) seen when a disc filled with counterphase rows of vertical bars is surrounded by a concentric ring filled with counterphase rows of horizontal bars. The effect is paradoxical in that the disc appears to float relative to the ring but there is no concomitant awareness of displacement. We have discovered four new facts which may help elucidate how ocular fixations interact with spatial and luminance information to yield such PM effects. (1) Retinal adjacency is necessary. In dichoptic presentations (for instance, disc to the left eye and ring to the right eye), the PM effect is not seen, whereas it is readily seen monocularly. (2) Retinal inclusion controls which part of the pattern carries the PM effect. Upon adding a second, external ring with bars having the same orientation as those on the disc, the disc stabilises and the first ring begins to float. Placing the first ring on a different stereoscopic plane from the other two surfaces does not alter this outcome. (3) A difference in the orientation of the bars is not necessary. A weak form of the PM effect can be seen in patterns with bars of equal orientation but different contrast or spatial frequency. In these cases, the bars appear to drift in a direction normal to the main orientation of the bars rather than float. (4) The effects of orientation, contrast, and spatial frequency can be combined to construct especially striking PM effects. Stereoscopic depth separation also seems to facilitate the perception of paradoxical motion.

◆ Structure from motion in a moving and by a static observer: a comparison

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Theoretical descriptions of the structure-from-motion (SFM) effect often start with retinal motion as the only source of input. Nonvisual information is omitted most of the time in these analyses; however, most animal species also use nonvisual information in determining three-dimensional aspects of the world.

We compared human performance in three tasks involving the perception of three-dimensional structure from motion under two conditions: HM, with head movement and a static object; NHM, no head movement, but with a moving object. In both conditions, the random-dot-kinematogram stimulus was designed in such a way that retinal flow would be identical. The three tasks involved (i) rating and discrimination of surface slant, (ii) discrimination of surface curvature, and (iii) discrimination of surface curvature with limited-lifetime displays. Additionally, we measured motion-detection thresholds (iv) to examine whether head movements affect the accuracy of motion perception. The rating of surface slant was equal in both conditions.

Since static observers can only determine surface slant up to a constant factor, they probably assume some object rotation in the NHM condition. Discrimination of surface slant did not show significant effect of head movements. Moving observers were significantly better than static observers in discriminating surface curvature (Weber fractions: HM 20%, NHM 35%). Head movements significantly shortened the temporal integration process in SFM by 1 stimulus frame (16 ms) on average. Motion-detection thresholds were not affected by head movements.

These results indicate that information about ego movements enters the SFM process after motion detection and velocity-gradient detection. Therefore, we discard the possibility that proprioceptive information is only used as a retinal stabilisation factor during ego movement. The nonvisual information is probably used quantitatively to scale or calibrate the motion parallax.

◆ **Contrast/threshold ratio determines perceived velocity of Fourier and non-Fourier motion**

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We measured how the perceived velocity of a local target depends on target contrast, target velocity, position in the visual field, and type of motion ('Fourier' and 'non-Fourier' motion). Fourier motion consisted of a smoothly moving two-dimensional Gaussian envelope. For non-Fourier motion this envelope was modulated with a high-spatial-frequency carrier which remained stationary. We also measured contrast thresholds for direction discrimination for both types of motion.

To measure perceived velocity, human observers adjusted the velocity of a moving target (A) to that of a second target (B) so that the velocities of A and B were matched perceptually. We tested four conditions for each target: two types of motion (Fourier/non-Fourier) and two positions (foveal and 3 deg peripheral). Of the sixteen possible cross conditions, eight were tested (when A matched B, then B matched A) as a function of the contrast of B. First, a target was perceived to move more slowly when presented in the periphery than when presented foveally. Second, at equal physical contrast, non-Fourier motion was perceived to drift more slowly than Fourier motion. Third, the perceived velocity of a target increased with target contrast.

A two-alternative forced-choice procedure with a method of constant stimuli was used to measure the contrast thresholds for direction discrimination. Thresholds are defined as the contrast for 80% correct responses, and were measured for all four possible target conditions. Direction-discrimination thresholds were higher in the periphery than in the fovea and (for our choice of stimuli) higher for non-Fourier motion than for Fourier motion.

The contrast dependence of perceived target velocity on target contrast (physical) varies widely for the different conditions. Interestingly, however, when the target contrast is scaled to multiples of threshold, results from all conditions collapse onto a single contrast-gain function.

ELECTROPHYSIOLOGY AND CLINICAL RESEARCH

◆ **Coherent neurophysiological (VEP) responses of inferior parietal lobule (IPL) to spatial vision cognate stimulus attributes in man**

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The role of primate inferior parietal lobule (IPL) in spatial vision is widely acknowledged. We have carried out a system-based study on stimuli that varied in attributes, assumed to relate to the high-level 'early vision' visuospatial function of the IPL. We investigated the dependence of IPL VEPs on spatial vision cognate properties of the following stimuli: (1) a horizontally rotated face, 45° or 90° to the right or to the left, and an 'unusual angle of sight' double rotation, upwards and horizontally leftwards or rightwards; and (2) attending displacement of one or two nodal items, the eye relative to the eyebrow, to the right or to the left, two eyes symmetrically, and eye to the right and mouth to the left, symmetrically. We used a 'full face' as control. Monopolar recordings were taken from five adults with twelve cranial striatal-peristriatal and parietal electrode arrays, IPL's supramarginal (Su) and angular and Cz leads. Subjects were instructed to fixate centrally a point on monitor nodal eye-eyebrow region and to 'attend' independently to stimuli displayed for 200 or 300 ms on a computer. Analysis was limited to the first 240 ms. Changes in VEPs were recorded from parietal leads, and could be related to early processing of the 'face stimulus', task-bound to presumed 'mental rotation', to the direction/degree of rotation, and to attending to the displacement. In contrast, Oz, peristriae, and Cz showed no such changes except for some relatable to 'features'. 'Full face'

control IPS early negativity was replaced for test by an early positivity, or, apparently depending on processing strategies ('object centred' and/or 'ego centred'), by a second positive wave component. Early positivity start latencies were around 60–80 ms, significantly shorter ($p < 0.01$) than 100 ms for the striate, mostly in angular but for coherent changes in Su leads. A fast pathway seems to be involved in the generation of this posterior parietal positivity (angular and supramarginal). These temporally and spatially coherent VEP changes observed in IPL, task-bound to processing of tests, support a generalised rotation response, differentiation of direction/degree of rotation and also of attending displacements; parallel processing of spatial vision attributes, by components of IPL; invariances to direction of 'rotation', ie angular encoding of rotation across angle of sight, or else attending invariantly leftward vs rightward displacement; generalisation (abstraction) as part of IPL high-order 'early vision'.

◆ **Rhythmic photic stimulation induces cataleptic reactions in WAG/Rij rats**

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Rats of the WAG/Rij strain show hundreds of spike-wave discharges per day and are considered as a model for generalised absence epilepsy (van Luijtelaar and Coenen, 1986 *Neuroscience Letters* 70 393–397). Electrocorticogram mapping (Neurokartograph, Scientific Medical Company MBN, Moscow) showed that the spike-wave discharges begin and attain their maximal voltage in 60% of the cases in the occipital areas. This prompted us to investigate the effects of rhythmic photic stimulation in chronically implanted WAG/Rij rats. During photic stimulation (3, 10, and 25 Hz for periods of 2 min) the animals showed some behavioural signs of fear and the electrocorticogram was periodically driven by the rhythm of the flashes, but augmentation of the paroxysmal discharges was not observed. However, in the course of the first 5 min after the end of the visual stimulation in ten of the thirteen WAG/Rij rats a cataleptic state lasting up to ten minutes gradually developed, ie the muscle tone decreased, the animals became motionless and they could retain an uncomfortable pose when forced to sit on their sacrum. Spike-wave discharges were gradually augmented and were maximally expressed 5–10 min after the end of the photic stimulation. In the three remaining rats, the duration of the cataleptic state lasted 10–15 s. Control rats, seven Wistar, remained active after rhythmic visual stimulation and they did not manifest any sign of pathology in behaviour or in electrical cortical activity.

It can be concluded that genetically epileptic rats are highly susceptible to the induction of a cataleptic state, suggesting that the mechanisms responsible for spike-wave discharges and for catalepsy might be related.

◆ **On-off stimulation optimises the relationship between contrast sensitivity and VEPs in normals and amblyopes**

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Steady-state visual evoked potentials (VEPs) generated by contrast-reversal stimulation are frequently used to assess vision. However, when a range of spatial frequencies is employed, the resulting curve of VEP amplitude versus spatial frequency is a poor predictor of visual function. This is due to the presence, in most subjects, of a notch in the middle spatial-frequency range. If on-off presentation is employed a VEP-versus-spatial-frequency function results which resembles the contrast-sensitivity function and may therefore be a better index of visual function (Remky et al 1990 *Investigative Ophthalmology and Visual Science, Supplement* 31 256; Strasburger et al, 1993 *Clinical Vision Science* 8 211–234). In the present study we investigated the spatial-frequency dependence of contrast sensitivity and the VEP by using on-off and reversal at a range of temporal frequencies (12–20 Hz). We demonstrated that the relationship between the contrast-sensitivity function and VEP-amplitude-versus-spatial-frequency function is optimal with 16 Hz on-off presentation. In addition we described a population of amblyopes in which this method gives a better prediction of contrast sensitivity defects than does reversal.

◆ **Processing of color information in area V2 of the macaque**

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We investigated the representation of color in cortical area V2 of macaque monkeys. It is widely assumed that information about color is processed in parallel with information about

motion and form in the brain. In area V2, in particular, these parallal pathways are assumed to correspond to the thin, thick, and interstripe regions, as determined by cytochrome-oxidase (CO) staining. We recorded from single cells in area V2 of cynomolgus monkeys by means of standard acute recording techniques. After measuring the spatial and temporal properties of each cell, we performed several tests of its chromatic properties by means of sine-wave gratings modulated around a mean gray background and colored bars on a black background. The tissue was stained with CO to determine the stripe-compartmental location for each neuron. We also used Cat-301 immunoreactivity to identify more reliably the stripes associated with the magnocellular pathway.

For half of the cells the response showed a dependence on stimulus color. Unlike for neurons in area V1, the response of these neurons was generally poorly described by a model in which a linear combination of cone signals is assumed [Derrington et al, 1984 *Journal of Physiology (London)* 357 241–265]. Cell activity could be excited or inhibited by stimuli within a narrow range of color–luminance combinations. No particular color directions were preferentially represented. Cells showing color specificity could be found in any of the CO compartments, even though the most clearly color-opponent cells were predominant in the thin stripes. There was no correlation between color-selectivity, direction selectivity, and endstopping. The segregation of information in V2 is much less precise than previously reported, with color not only represented in compartments thought to be devoted to motion or form, but also in combination with the other stimulus attributes.

◆ Neural correlates of chromatic-contrast analysis

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Contrast sensitivity (CS) for chromatic isoluminant gratings differs from that for luminance-modulated (achromatic) gratings if chromatic aberrations are eliminated (Mullen, 1985 *Journal of Physiology (London)* 359 389). Spatial and temporal resolution limits for red/green and blue/yellow (tritan axis) gratings are lower than for achromatic gratings and are closely matched. Chromatic resolution remains lower than achromatic, even when cone-contrast correction is applied. Coarse chromatic gratings, presented to both eyes in a spatial antiphase, elicit no percept of stereopsis [as do similar achromatic patterns (Kulikowski, 1991 *Ophthalmic and Physiological Optics* 12 168)], but rather one of chromatic rivalry.

When chromatic aberrations are not eliminated, both spatial and temporal resolution for chromatic gratings increases. The corresponding cone-contrast-corrected CS functions merge into the achromatic CS curves. Under such conditions, fine gratings still look chromatic, but veridical colours are no longer seen, as though units detecting such patterns were only partly chromatic sensitive. Coarse gratings are less affected and chromatic rivalry still predominates for such patterns binocularly viewed in spatial antiphase; but the introduction of more edges (a chromatic chequerboard) facilitates fusion and stereopsis.

The above psychophysical observations are correlated with the characteristics of single-unit responses in the striate cortex of the rhesus monkey recorded with a tungsten microelectrode under light anaesthesia. All single units with strictly defined colour opponency had concentric receptive fields, low spatial and temporal resolution, and were monocularly activated (as compared with end-stopped chromatic units), which is consistent with the psychophysical findings. We conclude that the colour-opponent mechanisms giving rise to colour percepts at detection thresholds (Mullen and Kulikowski, 1990 *Journal of the Optical Society of America A* 7 733) are subserved by distinct neural populations. Other phenomena, which show different characteristics for red/green and blue/yellow channels, must result from colour-opponent and luminance-channel interactions, which may represent a separable stream processing chromatic textures and supporting stereopsis.

◆ Oscillatory responses in the cat LGB stimulated with binary and shaded images

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Oscillatory responses of cat lateral geniculate body (LGB) neurons stimulated by images of binary (sector, cross) or shaded (cylinder, toroid) geometrical figures were analysed. The stimulus was presented in different positions within an $N \times N$ matrix ($N = 10–15$) which was superimposed on the receptive field of the neuron. The dominant periodicity of the neuronal response was estimated by a Fourier transformation of the autocorrelation function of each poststimulus histogram. Three main domains of dominant frequencies (15–25 Hz, 30–70 Hz,

85–100 Hz) were revealed in 25%–30% of all histograms. These domains are similar to three types of oscillations in cat retinal horizontal-cell activities (Foerster et al, 1977 *Experimental Brain Research* **29** 347–366). The oscillations in the neuron responses to shaded stimuli varied in the range of 30–70 Hz and the frequency variation was correlated with the shade distributions, supporting our previous data (Podvigin et al, 1992 *Naturwissenschaften* **79** 428–431). When binary images with constant brightness were presented, the dominant frequencies of oscillations were about 40 Hz and did not vary at all or varied in a narrow frequency domain (± 5 Hz). The oscillations with frequency above 80 Hz were mainly observed in the neuronal activity, when the edge of the figure was placed inside the receptive field, or when the figure was presented near the receptive field. Thus, oscillation frequencies are shown to be influenced by the spatial distribution of brightness in the image; this observation supports the hypothesis of the functional role of 30–70 Hz oscillations in the synchronisation of the LGB neuron activities during visual perception.

CLOSING SESSION

◆ Linking propositions and the phenomenon of stopped motion

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Under some conditions, the perception of motion is severely compromised for isoluminant chromatic stimuli. I report conditions under which moving stimuli appear stationary (stopped motion). Possible linking propositions involved in explaining the phenomenon of stopped motion are explored.

◆ Mathematics and visual perception

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Some of the most fundamental problems in visual perception can only be adequately addressed within a mathematical framework. In this review four such problems are considered.

(1) What is the nature of the visual representation of the external spatial world? Since Lotze and Helmholtz, the need for an axiomatic approach has been evident, but, apart from suggestions that visual space may be hyperbolic, there have been few attempts to construct a systematic internal visual geometry. Such a geometry is likely to require both differential-geometric and spatial-order structures, and in one approach 'fuzzy' location descriptors have been used to construct geometric relations such as collinearity, straightness, and tangency [Ferraro and Foster, 1994, in *Shape in Picture* Eds Y-L O et al, NATO ASI Series (Berlin: Springer) pp 333–342].

(2) How are the motions of objects represented within this visual space? Two natural (Riemannian) metric structures on the space of object motions predict different minimal paths; the paths measured experimentally suggest that the simplest perceived motions have less to do with Newton's laws of motion than with the properties of visual flow fields (Carlton and Shepard, 1990 *Journal of Mathematical Psychology* **34** 127–188).

(3) How are objects recognised independently of their positions and orientations with respect to an observer? Insofar as recognition is independent of position and orientation (for rotations in the frontoparallel plane it is generally not), two complementary schemes have been developed for explaining shape perception, the one based on extracting invariants, the other on applying internal 'restoring' transformations [Foster, 1991, in *Pattern Recognition by Man and Machine* Ed. R J Watt (Basingstoke, Hants: Macmillan Education) pp 50–68]. In both schemes, the theory of continuous transformation groups (Lie groups) has been exploited, although the limitations of human recognition performance suggest that qualitative and fuzzy invariants (and the corresponding transformation groups and sets) may be more relevant quantities.

(4) How do internal representations of space, object motion, and object shape maintain their stability and their compatibility with visual experience, despite, for example, changes in the optics of the eye? In one explanation it has been assumed that the internal visual geometry is adaptive, thereby avoiding the problem of explicit recalibration; in another it has been assumed that this geometry is, by construction, invariant under smooth distortions of the image, although this constrains the types of structure that might be used by the visual system (Dodwell, 1994 *Spatial Vision* **8** 9–17).

All four problems are clearly interrelated, yet they have often been analysed independently, or, in the wider literature, without recognition of their basic mathematical character.

POSTERS: FIRST SESSION

SHAPE, TEXTURE, AND DEPTH

◆ Compression-magnification disparities and the perception of surface slant

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A vertical compression of the image in one eye relative to that in the other produces an impression of a surface slanted about the vertical axis (Ogle, 1938 *Archives of Ophthalmology* 20 604-623). This phenomenon is known as the induced effect. Recently, we reported that perceived inclination of a surface about the horizontal axis depends on the horizontal shear disparity extracted locally relative to the vertical shear disparities extracted globally (Howard and Kaneko, 1994 *Vision Research*, in press). We think that an analogous system to the shear disparities can be applied for the case of compression disparities. The purpose in the present study is to examine a theory for the induced effect, which states that the perceived slant of the surface depends on the horizontal compression disparity extracted locally relative to the vertical compression disparity extracted globally.

Computer-generated displays of random dots were rear projected on screens 60 deg wide and combined stereoscopically. Three types of compression disparity were introduced into the display—horizontal compression, vertical compression, and overall compression (vertical and horizontal compression of the same sign). Five kinds of stimulus configuration were tested—60, 30, and 10 deg wide with black surround, 10 deg wide with zero-disparity surround, and the dots distributed only on the horizontal and vertical meridians. Subjects set an unseen manual paddle to match the perceived slant of the stimuli about the vertical axis.

For the stimuli with small compression disparity ($<2\%$), the amounts of perceived slant of 60 deg isolated display with vertical compression disparity was nearly the same as those with horizontal compression disparity. For the stimuli with zero-disparity surround, on the other hand, the vertical compression disparity produced no slant and the overall compression disparity produced greater slant than for isolated stimuli. These results support the hypothesis that perceived slant of each local area is derived from the difference between the local horizontal compression disparity and the global vertical compression over the binocular field as a whole.

◆ Multiplicative/additive combination rules towards transparent-stereoscopic-slant perception

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In visual motion, Stoner et al [1990 *Nature (London)* 344 153-155] report that two superimposed square-wave gratings of different orientations may appear to move coherently or independently, depending on the luminance of the intersections: when the luminance of intersections are consistent with a multiplicative combination rule, humans tend to observe the two square-wave gratings sliding over each other in a percept of motion transparency. When the intersections are inconsistent with a multiplicative combination rule, motion coherence is perceived. Similarly, when confronted with two stereoscopic views of the world, the human visual system must decide whether or not the two retinal images arise from single or multiple objects. Here we report that similar combination rules are present in the processing of transparent stereoscopic images. Subjects were presented with stereoscopic images composed of superimposed square-wave gratings that were near horizontal and vertical in orientation. The stereoscopic transformation was consistent with a single surface sloping away from the viewer. By varying the brightness intensity of the intersections of the luminance patterns only, subjects reported the percept of either a single slanted surface or two transparent surfaces (one fronto-parallel, the other sloping away from the viewer). Unlike the case of visual motion, conditions for perceived transparency occurred only when the luminances of intersections were consistent with a multiplicative/additive combination rule of square-wave components.

We conclude that the human visual system utilises similar tacit knowledge in the processing of both motion and stereoscopic transparency. However, the stereoscopic percept of transparency is strongly influenced by figure/background assumptions.

◆ Second-order derivatives in the extraction of three-dimensional shape from optic flow

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Recently, we have shown how a complete set of measures of three-dimensional shape can be derived directly from the velocity field generated by a rigid curved surface patch under perspective projection. We used invariance under rotation of the image plane to decompose the second-order velocity field in differential invariants. An assumption of this model [and several

others (Droulez and Cornilleau-Pérès, 1990 *Biological Cybernetics* **62** 211–224; Koenderink and van Doorn, 1992 *Journal of the Optical Society of America A* **9** 530–538)] is that shape can be detected from second-order spatial derivatives of the velocity field. In this study we have tested this assumption experimentally.

We reasoned that if second-order spatial derivatives are important for perception of shape then discrimination should become difficult when the second-order derivatives are selectively corrupted by noise and to a much smaller extent by other types of noise. We showed subjects pairs of surface patches rotating in depth and the task was a two-alternative forced-choice discrimination between the planar and nonplanar patch. To the velocity field we added noise which was temporally white but spatially structured as a differential invariant. We added zero-order, first-order, second-order, and third-order noise. The noise strength was scaled so that the integral of the magnitude of the noise velocity field over the viewing area was constant. Generally, we found the highest discrimination thresholds for second-order noise, thus confirming that second-order spatial derivatives are important for shape discrimination. Also, within the first order we found large differences—the deformation has a much stronger effect than rotation or divergence.

◆ **Interaction of monocular and binocular cues in pictorial relief**

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We studied the interaction of monocular and binocular cues in pictorial relief. The stimuli were monochrome photographs of gray-colored lifesized human torsos covered with a mottled texture. For binocular viewing conditions we took stereophotographs from a distance of approximately 2.5 m with a stereo base of 7 cm; for the monocular viewing condition single photographs were taken from the midpoint of the stereo base. The photographs were presented on a CRT screen; for binocular viewing a stereoscope was used that simulates convergence at infinity. We prepared two types of views—one with very flat frontal illumination that clearly revealed the surface texture and also the contour due to an even background at a slightly different tone, the other with an ‘arty’ studio illumination designed to reveal the shape clearly and a graded background designed to suggest the spatial isolation of the torso from its ambience. In both cases the stereo information was identical. The monocular cues were as different as could be, resulting in a very striking difference between the photographs. Four subjects participated in the experiments. We used a surface-attitude probe to measure pictorial relief. As expected, the shading had a decisive influence on monocular relief, but rather less so on binocular relief. However, we found that the qualitative structure of binocular relief was very sensitive to the shading. Apparently monocular cues often override the disparity information. These ‘monocular corrections’ on the binocular stereopsis typically rotate the thorax with respect to the pelvis or the extremities with respect to the trunk in pictorial space.

◆ **Depth perception from motion parallax in peripheral vision: dependence on the perception of relative velocity**

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The depth perception produced by motion parallax, which is one of the visual depth cues, is stated to be related to the perception of relative motion among moving objects in observational situations with and without head movements (Rogers and Graham, 1979 *Perception* **8** 125–134). The purpose in this study was to investigate the relation of perceived depth from motion parallax to the perception of relative velocity in peripheral vision. In experiment 1, identical stimuli that simulated three-dimensional surfaces (equivalent disparities 15 min and 3 min) were presented at various eccentricities (0, 5, and 15 deg) in the visual fields of observers when they moved or fixed their heads. The amounts of perceived depth decreased with eccentricity, except that the difference between that for 0 and 5 deg eccentricity was not significant in viewing the display with equivalent disparity of 3 min without head movements. When this display was viewed peripherally, perceived depth with head movements was smaller than that without. These results were examined in relation to the perception of relative velocity in experiment 2. First, the perception of relative velocity at each eccentricity was measured individually. On the basis of the results of this measurement, motion-parallax stimuli, which were expected to produce the equivalent relative-velocity perceptions among eccentricities, were presented. As a result, the perceived depth decreased linearly with eccentricity. Differences between results with and without head movements were not found. It may be possible to explain the difference

in perceived depth between observational situations in experiment 1 on the basis of the difference in sensitivity to relative velocities. These results suggest that perceived relative velocity is a determinant of the perceived depth from motion parallax. But if the relative velocities were perceived as equal, the depth perceived from them decreased with eccentricity.

◆ **Time-dependent perception of large-field disparity gradients: validation of a model for slant perception during dynamic viewing**

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Slant perception on the basis of disparity requires a reference for distinguishing between absolute disparity (without reference, fixation dependent) and relative disparity (with reference, fixation independent). We have investigated the influence of presentation time on slant perception in the presence and in the absence of a reference in the case of dichoptically presented large-field stimuli (70 deg × 70 deg). The stimuli contained randomly and sparsely distributed circles (diameter 1.5 deg). Subjects had to judge the slant of a disparity gradient presented for either 500 ms or 10 s. The disparity gradient was either horizontal or vertical. For horizontal disparity, perceived slants in the 10 s 'without-reference' condition were roughly twice as large as in the 500 ms 'without-reference' condition; thus, 'without-reference' slant builds up slowly. However, slants found in the 10 s and the 500 ms 'with-reference' conditions were judged to be similar; thus, 'with-reference' slant builds up rapidly. For vertical disparity, slants were perceived in the 10 s 'without-reference' condition, whereas no slants were perceived in the 500 ms 'without-reference' condition or in the 500 ms and the 10 s 'with-reference' conditions. Thus, without a reference, vertical disparity is used for slant perception but slant builds up slowly, whereas with a reference, vertical disparity is not used for slant perception. These results validate an important aspect of our model for slant perception under dynamic viewing conditions. According to this model absolute translational and gradient disparities are poorly perceived because they provide unreliable information; namely, instead of being caused by the stimulus the disparities could also be caused by eye or head movements. We suggest that perception of absolute disparity involves a recalibration process (the slow buildup), which lets a distinction be made between object-induced and head-induced gradients. This in turn can explain the well-known adaptation to slant.

◆ **Evidence for monocular determinants of plaid coherence and direction**

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There is mounting psychophysical evidence that the processing of two-dimensional motion is carried out by at least two different processes. One of these is a two-stage process which appears to integrate one-dimensional component signals in a manner consistent with the intersection-of-constraints (IOC) algorithm (Burke and Wenderoth, 1993 *Vision Research* 33 343–350), and a second is a low-level, monocular mechanism (Alais et al, 1994 *Vision Research*, in press) responding directly to the motion of the physical intersections in two-dimensional displays (the 'blobs'). Two experiments are presented which extend these findings. In the first, it is demonstrated that prior exposure to a similarly drifting grating or plaid can substantially raise the coherence threshold of a test plaid, but only if the adaptation and testing is of the same eye. The elevation of the coherence threshold is much more modest if the test plaid is presented to the unadapted eye, suggesting that the perceived coherence of a drifting plaid is largely under the control of a monocular mechanism. Similarly, in a second experiment in which perceived plaid direction was examined, monocular adaptation to a drifting plaid is found to alter post-adaptation direction judgments only when the adaptation and testing are of the same eye. The results of these experiments provide strong evidence that a monocular process, in contrast to the binocular mechanisms presumed to underlie the IOC process, is involved in determining both the perceived direction and the coherence of drifting plaids.

◆ **A computational model for stereoscopic slant based upon orientational differences of Fourier and non-Fourier mechanisms**

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In visual motion, Chubb and Sperling (1989 *Journal of the Optical Society of America* 79 1986–2007) constructed drift-balanced motion stimuli in which there is no direct image-intensity correspondence between successive time frames, and yet motion is still perceived. Chubb and Sperling suggest that these stimuli may not be understood in terms of their Fourier spectra. In contrast to Chubb and Sperling, Fleet and Langley (1994 ARVO) suggest that the

motion of some drift-balanced stimuli may be characterised in the frequency domain by the orientation of peaks of power relative to the origin, and the local orientation of power. One method by which these two orientations may be extracted is via the phase and amplitude response taken from quadrature bandpass filters. In this case the orientation of phase would correspond to a Fourier mechanism and the orientation of amplitude a non-Fourier mechanism.

In stereopsis, Koenderink and Van Doorn (1976 *Biological Cybernetics* **21** 29–35) suggest that the human visual system may utilise the orientational differences between stereoscopic views towards the perception of surface slant. Here we wish to establish whether or not orientational differences from similar processes to motion might be employed by humans towards the perception of stereoscopic slant. We first demonstrate that stereoscopic slant may be inferred by an affine transformation to two-dimensional amplitude-modulated sinusoidal patterns. The patterns generated were such that the carrier was oriented horizontally and the beats near vertically. These findings were then modelled by an algorithm that extracts both amplitude and phase information from each bandpass-filtered stereoscopic image and extracts the orientational differences to obtain a measure of surface slant.

◆ **What visual mechanisms mediate judgments about textures?**

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How are judgments made about the spatial scale or frequency content of patterns, such as textures, which contain components at multiple orientations? Are judgments based directly on the signals of pathways tuned to the individual orientations? Or are judgments based on the responses of higher-order texture mechanisms, such as the one demonstrated by Olzak and Thomas (1992 *Vision Research* **32** 1885–1898), which sum signals across orientations? We use an uncertainty paradigm to address this question. The observer discriminates between plaid patterns, each of which is formed by superimposing vertical and horizontal sinusoids. On every presentation, one of these two sinusoids has a spatial frequency of 4 cycles deg^{-1} and the other, the cue, a frequency which is slightly higher or lower. The subject classifies each presentation as having either the higher-frequency or lower-frequency cue. In the certainty condition, the orientation of the cue (vertical or horizontal) is fixed; in the uncertainty condition, the orientation is randomly varied from trial to trial. If judgment is based directly on signals from pathways tuned to the individual orientations, the uncertainty about which orientation carries the cue will reduce performance. If judgment is mediated by higher-order mechanisms which sum signals across orientations, the uncertainty should have no effect. The results are that uncertainty does reduce performance, but by a smaller amount than found in parallel control experiments in which the uncertainty is about the dimension of the cue (contrast or spatial frequency) rather than the orientation. These results, in combination with results of earlier discrimination studies, suggest that observers use information both from the orientation-tuned pathways and from higher-order summing circuits and argue against a strictly hierarchical view that decision processes have access only to the signals of higher-order mechanisms.

◆ **Stroboscopic vision: a comparative study**

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The work of MacKay [1958 *Nature (London)* **181** 506] led me to examine how strobe lighting would affect the perceptual organization of a pattern of moving dots. Under normal steady illumination, the dots moving in a direction opposite to the surround were grouped by the 'common-fate' factor of the Gestalt law and were perceived distinctly separated from the rest. Under strobe lighting at flash rates less than 12 Hz, the moving dots changed the perceptual grouping to the 'spatial nearness' one. In the latter situation the dots moving in the opposite direction to the surround were seen embedded in the background and could not be easily recognized (Sumi, 1990 *Perception* **19** 390). Similarly, how strobe lighting would affect the prey-catching behavior (PCB) of the toad was examined. At flash rates down to 4 to 6 Hz, the PCB of each of two toads (*Bufo japonicus formosus*), three to five years old, was successful. At 3 Hz and less, their PCB failed, and they could only fix their gaze in the direction of the prey. Even if the prey moved around, the toads could not follow the movement with fixed gaze. At 3 Hz or so, however, their PCB succeeded against prey moving towards them but failed against prey moving away from them.

By adding one strobe flash to the other successively, the exposure time of moving stimuli could be prolonged. In human vision, at a strobe flash rate of 8 Hz, perceptual 'common-fate' grouping of the moving dots might be completely destroyed but could be recovered again with

an increase of their exposure time to 50 ms. In the case of the toads, at a flash rate of 1 Hz, their PCB became more successful as the exposure time for the moving prey increased, but did not recover completely until the exposure time was extended to 90 ms or so.

◆ **Small chromaticity differences and stereopsis**

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Stereopsis can be evoked by stimuli defined solely by chromatic differences [de Weert and Sadza, 1983, in *Colour Vision* Eds Mollon and Sharpe (London: Academic Press)]. This view is not generally accepted but is supported by the present experiments with stimuli characterised by small differences in chromaticity. In previous studies, only large colour differences had been employed. Thirty-three vertically oriented, narrow coloured stripes were fixed on a 10 cm × 10 cm square plate. In terms of the Munsell notations, all stripes were of the same value but either hue or chroma was different in three of the stripes. One of these differently coloured stripes formed the centre of the pattern, whilst the other two flanked it slightly asymmetrically. The stripe pattern was illuminated by daylight and was viewed binocularly at a distance of 1 m through a prism system causing a right-left reversion for the right eye. This arrangement produced a horizontal, crossed or uncrossed, disparity of 10 min of arc for the two flanking stripes. Accordingly, they appeared to float either in front of or behind the central stripe, provided the colour difference was large enough. This observation was quantified in forced-choice experiments in which plates with different chromaticities for the depth stimuli but identical chromaticities for the background stripes were used. The observer determined the sign of disparity. The percentage of correct responses increased significantly with increasing differences in chromaticity, and a threshold for stereopsis was defined in terms of chromaticity difference. In two independent experiments where either hue or chroma was varied, the threshold values equalled about 5.5 times the just-noticeable difference of chromaticity as given by MacAdam [1985 *Color Measurement* (Berlin: Springer)] for the chromaticity coordinates $x = 0.3740$, $y = 0.3074$ (hue condition), and $x = 0.3075$, $y = 0.4084$ (chroma condition).

◆ **How irrelevant are 'irrelevant' texture elements?**

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In experiments in texture segmentation the critical features that determine segmentation performance are sought. Orientation difference is one of these critical features. Usually the textures used in these experiments show the critical feature as 'pure' as possible (eg identical lines with different orientation in the target and context area). This approach can be useful if the influence of just this feature (in this case orientation) is to be examined. But in the 'real' world these pure conditions are rare. Psychophysical experiments were used to determine the influence of 'irrelevant' texture elements on segmentation performance. These irrelevant elements were placed just beside the critical elements, over the whole texture, including the target area. The textures were realised according to Fox and Mayhew (1979 *Perception* 8 75-91) and consisted of right angles of different orientation. The irrelevant texture elements were points, which were placed, depending on the condition, at different distances from the angles.

The results showed (1) that the 'irrelevant' points did have an influence on segmentation performance; (2) this influence was a performance increment or decrement, depending on the distance of the points from the angles; and (3) the influence of the distance of the points on performance varied with retinal eccentricity: if a performance increment was observed foveally, performance in peripheral areas decreased, and vice versa. The results can be explained by a mechanism of low-pass filtering, suggesting a perceptual fusion of adjacent elements leading to 'new' features. This fusion varies with retinal eccentricity, as low-pass filtering increases with eccentricity, and with interelement distance, as fusion is facilitated by smaller distances.

◆ **A tolerance analysis for structure-from-motion stimuli**

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We present a tolerance analysis for a large group of stimuli used in structure-from-motion tasks. A tolerance analysis can reveal to what degree the information for a task is available in the stimulus. Many authors regard the three-dimensional structure as input, whereas they should actually consider the sequences of two-dimensional images presented to the subject. Any realistic model of the visual system should incorporate a tolerance analysis as a complete

description of the stimulus. To perform the analysis we developed a method of obtaining the optimal rigid three-dimensional point configuration of an (unlimited) number of frames.

As an example we apply this analysis to the experiments of Norman and Todd (1993 *Perception & Psychophysics* 53 279–291). Objects were shown under orthographic projection which rotated and, at the same time, stretched in one dimension. In the case when stretching was in the viewing direction, observers perceived a rigid object rotating with varying angular velocity. A nonrigid object was perceived when stretching was in a direction orthogonal to the viewing direction. Our tolerance analysis shows that deviations from the optimal rigid solution for stretching in the viewing direction are rather small (standard deviation in the projected point positions of about 3 min of arc). Moreover, these deviations appear to be larger than the deviations introduced by using orthographic instead of perspective projection. The optimal rigid solution rotated with varying angular velocity, which is in accordance with the findings of Norman and Todd. For stretching in the perpendicular direction no reasonable rigid solution exists. The analysis explains the qualitative findings of these experiments, thus illustrating that the empirical findings are to a large extent due to stimulus limitations rather than to mechanistic properties of the visual system.

◆ **Metamerisms in structure-from-motion perception**

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Under parallel projection, the structure and three-dimensional motion of a moving rigid object are fully specified by the projected positions, velocities, and accelerations of its identifiable points. When accelerations are not or are inaccurately known, however, the structure and three-dimensional motion of the object are only specified up to a one-dimensional metamer class of solutions. For example, slanted planes that rotate in space have identical projected positions and velocities (and are thus theoretically metameric) when the turn (the magnitude of rotation) is a specific function of the slant and tilt of the plane. If the human visual system does *not* exploit the acceleration information, then this metamer class may exist perceptually. We tested whether such families of metameric moving planes indeed exist.

Observers viewed a ten-frame motion sequence of a vertically slanted plane (textured with random dots) oscillating around a vertical axis. A square window covered the contours of the moving plane. A similarly moving plane was shown spatially separated from the first one. The observer's task was simultaneously to match the (initially random) amounts of rotation and slant of the second plane with those of the first plane. No feedback was given. The data indeed show that matched slant–turn combinations are not unique for a given moving plane, even for large amplitudes of oscillation (eg turn 80° and slant 45°), but that they can differ widely from trial to trial, forming a one-dimensional metamer class. The experimental relation between matched slant and matched turn within a metamer class is consistent with the theoretical relation (approximately hyperbolic) expected when the projected acceleration is not input to structure-from-motion computations.

◆ **Aftereffect of relative motion produces motion in depth**

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A stimulus that is changing its size produces a perception of motion-in-depth. Similarly, a motion aftereffect produced by the same stimulus also produces a perception of motion in depth. Moreover, presenting subparts of an inducing stimulus, such as the two opposite edges, as a test stimulus is sufficient to produce an aftereffect of motion-in-depth. In this study, we examined the spatial and temporal properties of the induction stimulus for the aftereffect of motion in depth. In experiment 1, we used two vertical lines that subtended 1 deg for the induction and the test stimuli. There were six different distances between the two test lines, ranging from 1 to 3 deg. There were six corresponding pairs of induction stimuli which moved away from each other in the slow phase of a sawtooth waveform. The average position of the line corresponded to the position of the test stimulus. Each line moved 0.2 degree with a velocity of 3.33 deg s⁻¹. After adaptation for 3 min, two stationary test lines were presented. In general, the vertical lines were first perceived to be approaching each other (two-dimensional motion aftereffect), and subsequently, these two stimuli were perceived to be moving away from the observer (three-dimensional motion aftereffect). These aftereffects continued for 25–35 s. This general effect was smaller when the distance between two lines was larger and disappeared when the distance between the two lines was 3 deg. In experiment 2, we examined the effect of presenting the two induction stimuli sequentially. The two-dimensional motion aftereffect was

induced but not the three-dimensional one found in experiment 1. These results suggest that what has been called the 'changing-size' or 'looming' cue to depth has a subcomponent, namely, a relative motion in the opposite direction.

◆ **Occlusion provides depth-order information but camouflage does not in the Wheatstone-Panum limiting case**

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The Wheatstone-Panum limiting-case stereogram which presents one image on one retina and two images on the other retina produces a three-dimensional impression. The order of perceived depth has been reported to be consistent with the prediction of the occlusion hypothesis (Ono et al, 1992 *Perception & Psychophysics* 51 3-13) and with that of the camouflage hypothesis (Howard and Ohmi, 1992 *Investigative Ophthalmology and Visual Science, Supplement* 33 1370). We examined the order and the magnitude of perceived depth in two conditions; one image on one retina is presented so as to fuse with the temporal image on the other retina in the first condition and with the nasal-side image in the second condition. The occlusion hypothesis predicts that the fused image is seen in front of the nonfused image in the first condition, whereas the camouflage hypothesis predicts that the fused image is seen behind the nonfused image in the second condition. The horizontal separation between the fused and nonfused images was varied from 10 to 30 min of arc in both conditions. Sixteen subjects were asked to report verbally the order and the magnitude of perceived depth of the stereogram. The fused image was reported to be seen in front of the nonfused image in the first condition but it was not reported to be seen behind the nonfused image in the second condition. The mean magnitudes of the perceived depth did not covary with the horizontal separation in either condition. The results suggest that the occlusion provides depth-order information but not depth-magnitude information and the camouflage provides neither type of information in the Wheatstone-Panum limiting case.

◆ **The depth-scaling parameter for two-frame motion**

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The twofold goal in this study was to determine how depth is recovered in the case of two-frame motion and whether depth reconstruction is similar for motion and binocular stereopsis. Two orthographic projections of a moving solid are insufficient to reconstruct depth uniquely: the solution is a one-parameter family of equally legitimate three-dimensional (3-D) interpretations. Any 3-D motion can be decomposed to translation, scaling, rotation around viewing direction, and rotation around some axis in the frontal plane. Theoretically, all component parameters of this decomposition can be recovered from the comparison of two images, except one: the rotation angle of the last component. This angle is a good candidate for the parameter that controls the depth in 3-D interpretation. In my experiments I show that only the angle of rotation around the axis in the frontal plane affects the depth of the percept. Other motion parameters, including dot density and temporal parameters, had no effect on the depth (although they affected the quality of correspondence). The value of the angle with which the object was perceived veridically (ie the default rotation angle assumed by the visual system in the absence of additional information) varied between individuals over a wide range (about a factor of 10). Nevertheless, this default angle for each observer was the same (within measurement error) as the vergence angle at which stereoscopic depth was seen veridically. These results provide strong evidence for the existence of a structure-from-multiple-views mechanism that operates both in structure-from-motion and in binocular-stereoscopic tasks.

◆ **On the dynamics of Necker cube reversals**

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The perceptual instability of Necker's cube is characterised by spontaneous changes between two distinct perspectives, with the impossibility for the observers to stabilise their perception. For a rotating Necker cube, these changes of perspective translate into direction reversals. Naïve observers can thus be asked to specify the direction of rotation without being aware of a change in perspective. The purpose in this study was to determine how the perceptual oscillations elicited by a rotating Necker cube depend on the temporal characteristics of the stimulus, ie its angular speed and the introduction of a variable number of physical reversals of direction. The rationale for the latter was that fluctuations imposed on an unstable system may alter its overall dynamics.

Perceptual oscillations were stable for angular speeds of up to 25 rotations min^{-1} but increased by a factor of about 3 for 72 rotations min^{-1} . They were negatively correlated with the number of physical reversals. Because the intervals between a physical reversal and the perceptual reversal that followed were significantly larger than the intervals between two successive perceptual reversals, it is concluded that external perturbations of the system reduce its instability. An analysis of the perceptual oscillations as a function of the time elapsed from the beginning of an experimental session (1 min) reveals a progressive increase in the reversal frequency. Finally, the fact that (as revealed by a Fourier analysis) the train of reversals does not display any observable periodicity, whatever the experimental condition, suggests that the perceptual state is governed by random noise within the underlying system.

◆ **Texture segregation in the cat: interaction between orientation and contrast**

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The nature of the interaction between two texture-segregating parameters (contrast and orientation of texture elements) was studied in the cat. Texture segregation for line texture elements was assessed at three orientations (45° , 30° , and 22.5°) and three contrasts (33%, 42%, and 53%). The contrast of the texture elements was manipulated by reducing the percentage of pixels. A spacing of the texture elements of 2 deg was chosen because segregation based on orientation difference was optimal for that spacing texture (De Weerd et al, 1992 *Vision Research* 32 305–322). Texture-segregation performance was measured by means of a 73.5%-correct staircase procedure (Wetherill and Levitt, 1965 *British Journal of Mathematical and Statistical Psychology* 18 1–10) according to line length of the texture elements. The position of the square and the orientation or contrast polarity defining the square and background were randomised from trial to trial. Facilitatory interaction between orientation and contrast was only found near the contrast and orientation thresholds for texture segregation. For suprathreshold contrasts and orientation differences, contrast always dominated orientation differences in texture-segregation performance.

◆ **Pulfrich's string**

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It is surprising that the Pulfrich pendulum effect remains when the bob is tracked with the eyes and there is no reference marker. The stereo observed in this minimal-information condition could hardly be due to convergence.

When the usual string, swinging in an arc, is replaced by a string that remains vertical (actually a thin rod suspended from a parallelogram) the bob ceases to move in an apparent ellipse. It is now seen to move veridically, in a straight line normal to the observer. That is, no depth is seen without the usual arc of the string of the pendulum. Just what information the swinging arc provides is not yet entirely clear. But we should not ignore Pulfrich's string.

◆ **Recovering shape from texture: the effect of density**

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The texture pattern provides cues which can be used to recover the three-dimensional orientation of the surface. Although many cues are available in principle, the human visual system only uses a limited number of cues. A possible source of information is the density gradient. Because the density of texture elements increases as the surface recedes, the relative density of texture elements can be used to recover shape from texture. Density can be defined in different ways. Most commonly, density is defined as the area of the surface divided by the area of the elements covering the surface.

We manipulated the texture density of our stimulus surfaces in two ways. First, density was manipulated by increasing the distance between the texture elements, while keeping the size of each element constant. Second, density was manipulated by increasing the size of each texture element, while keeping the interelement distance constant. The surfaces, covered with the different kinds of texture pattern, were then slanted either to the left or to the right. Subjects had to decide whether the surface was slanted to the left or to the right, and the accuracy of their responses was measured. The results show that performance decreases with increasing density. Performance was, however, only affected by the first manipulation of density (ie varying the interelement distance), but not in the second manipulation (ie varying the size of the texture elements). The results perfectly match the predictions made by a shape-from-texture algorithm we constructed to model human texture perception. The model does not take the density gradient into account. With it we can only compute a generalised version of the compression gradient,

based on the shapes of the individual texture elements. The accuracy of the gradient increases as the distance between the texture elements increases.

◆ **Segmentation of second-order textures defined by orientation by means of a multichannel gradient model**

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Differences in texture allow the segmentation of a scene into distinct areas. Those regions defined by the orientation of texture elements are particularly salient. Standard local-energy models have been applied with a fair degree of success in both motion and texture analysis [Bergen and Landy, 1991, in *Computational Models of Visual Processing* Eds Landy and Movshon (Cambridge, MA: MIT Press)]. One problem, however, with the Fourier-energy approach is that it does not allow the extraction of correct orientation in second-order stimuli. In these stimuli the mean luminance of the scene observed is constant, and hence it is necessary to look at the second-order statistics to extract the required information. The human visual system is able to extract orientation information from second-order texture patterns which casts doubt on the validity of standard energy models in this domain.

An alternative approach to the standard energy model is to use spatial gradients of image brightness. In the modelling of motion mechanisms we have shown previously that it is possible to construct a model by using spatiotemporal brightness gradients which is able to recover the direction of motion for second-order motion patterns (Johnston et al, 1992 *Proceedings of the Royal Society of London, Series B* 250 297–306). Using a modified version of this model we found we could segment a region of oriented texture elements from an oriented background texture both of which have constant mean luminance. Here we describe the operation of the model in the spatial domain and the results of computer simulations on a variety of textured patterns.

◆ **The possibility of multiple matching in the Panum limiting case**

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There are many papers dealing with the problem of stereoscopic vision when one eye sees two objects and the other eye sees only one (Panum limiting case). The fusion and depth seen in this case is still not understood well (Ono et al, 1992 *Perception & Psychophysics* 51 3–13). Our object was to verify the possibility of multiple matching under the Panum limiting case. Bars (20 min × 10 min) were presented on the CRT monitor. Polarised filters allowed one eye to see two stimuli and the other eye to see only one stimulus. One bar flickered at a frequency of 3–5 Hz. Besides the bars the subject saw the fixation cross. During the session both the location of the crosses on the screen and the distances between the two bars were changed. The subject specified how many stimuli (two or more) were seen, where they were perceived in space, and which was flickering. On the basis of the obtained results we draw the conclusion that there are possibilities both of unique and of multiple matching. If we speak about the perceived brightness of fused bars then unique matching takes place, but if we speak about the locations of the bars in space multiple matching is possible. We propose the following model. It consists of a huge number of parallel functioning local channels. Each channel obtains signals from the limited region of the retina (RF). The RFs of the channels significantly overlap each other and a single stimulus acts on many local channels. Despite local stereo channels receiving signals from only two RFs located in the corresponding region of the retinae, the position of a single stimulus in one retina, owing to overlapping of RFs, can impact on the perceived position of a few fused stimuli.

◆ **A simulation of orientation-contrast detection with Watson's Gabor-filter model**

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Orientation contrasts play an important role in the preattentive visual segmentation of textures. If the orientation contrasts between adjacent texture elements are sufficiently large, subjects detect a texture border very rapidly. Psychophysical experiments were used to determine how the extent of the orientation contrast and the retinal eccentricity of the presentation of the target texture influenced the probability of segmenting a target texture from its surrounding background texture. Results showed that the probability of successful segmentation was very low when the orientation contrast was less than 30°. The retinal eccentricity of the presentation, which was varied up to 10 deg to the left or right of the fixation point, resulted in an inverted-U-shaped course of the probability of detection with peak performance between 3 and 6 deg of eccentricity. A computer simulation was used to test whether the experimental data could be predicted within Watson's Gabor-filter model [1983, in *Physical and Biological*

Processing of Images Eds O J Braddick, A C Sleight (New York: Springer) pp 100–114]. Results showed a good fit with the experimental data when the simulation was based on a filter family with an 8 cycle deg^{-1} central filter surrounded by concentric rings of increasingly larger filters. Model predictions were even closer to the psychophysical data when Watson's fixed filter orientations were replaced by 'orientation-adaptive' filters. It is concluded that Watson's model provides a good starting point for a better understanding of preattentive visual segmentation phenomena.

◆ **Holistic perception of one-dimensional stimuli**

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Holistic perception of collinearly presented strings of dots was investigated in two experiments. The effect of dot spacing (regular, graded, or random), number of dots, orientation of the strings, and the spatial-order relations was studied. The adjustment procedure used required that the observers moved two distinct dotted strings till they formed a unitary percept, ie the place of linking of strings could not be recognised. The results showed that the main factor in task performance was the interdot distance of the dots nearest to the approaching end of the strings. The orientation and the spatial-order relations had no significant effect on performance. The dot spacing in the strings influenced the variability of the responses. Different models of perceptual grouping based on the proximity model of Van Oeffelen and Vos (1982) were fitted to the data. The role of short-range and long-range interactions is discussed.

◆ **Precues facilitate the perceptual organisation of dynamic random-dot patterns**

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Ball and Sekuler (1981 *Perception & Psychophysics* 30 119–128) showed that a briefly flashed line which primed the subject to the direction of motion improved detection of a low-contrast random-dot kinematogram. Our first aim was to study whether cues which themselves are random-dot patterns can reduce uncertainty about the direction of motion and to what extent the possible improvement can be explained by knowledge-based top-down processes. Our second aim was to study whether the visual system can integrate motion information of random-dot patterns, spatially dispersed among noise patterns, so that improvement in performance with increasing number of display frames can be found. Each stimulus display consisted of small apertures through which random-dot motion was seen. In each aperture the dots were moving in one of the four possible directions, and the task was to identify the quadrant that contained coherent motion. Both target duration (experiment 1) and cue lead time (experiment 2) were varied. Cues that indicated the direction of trailing coherent motion enhanced segregation, for all subjects. Enhancement was significant when the dots of cue patterns and target patterns were moving in the same or in the opposite directions. When the movements were in the opposite directions the signal-detection approximation (Peterson et al, 1954 *IRE Transactions on Information Theory* 4 171–212) underestimated the improvement, ie a gain in performance exceeded the gain that an ideal detector would exhibit. The results of experiment 1 also suggested that the motion information of dispersed kinematograms can be temporally recruited—performance asymptoted after approximately five displacements. The results of experiment 2 showed that, if cue lead time was long enough so that the subject could identify the cue motion at the 100% level, performance did not improve significantly as a function of cue duration.

◆ **Da Vinci stereopsis and figure-ground discrimination**

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The visual system uses ecological constraints about monocular-binocular discontinuities when producing a depth segmentation of a scene (Nakayama and Shimojo, 1990 *Vision Research* 30 1811–1825). The depth localisation of a monocular point can be determined by a depth-constraint zone caused by an occluding edge and a monocular area can even produce a percept of a subjective plane because it implicates the presence of a sharp depth discontinuity. We measured the effect of figure-ground discrimination on da Vinci stereopsis by using a binocularly viewed rectangular frame and monocular points. The frame was localised in convergent or divergent disparity ($\pm 49 \text{ min arc}$) and a monocular dot was in one of twenty-four possible places laterally to the inner or outer contour of the frame. The task of the subject was to position a depth probe to the apparent depth of the monocular point.

Our results show that a monocular point was perceived differently depending on its place inside or outside the binocular frame. When a monocular point was presented in the vicinity of

the external side of the frame, it was localised in divergent depth (approximately 40–50 min arc) and the frame appeared opaque. When the point was inside the frame, the percept was completely different and instead of sinking into the divergent depth the monocular point appeared as a part of the binocular frame. Our results suggest that when a monocular object is inside a figure the occlusion interpretation is in some cases ignored. This demonstrates that monocularity is not always interpreted as a depth discontinuity and thus the use of occlusion constraints is a more complicated process than previously thought.

◆ **Recognition of visual objects under conditions of angular rotation**

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Psychophysical experiments were carried out to study pattern perception under conditions of angular rotation. Stimuli such as letters were presented tachistoscopically for 10–40 ms. At first all stimuli had the orientation shown on a response card. Then rarely and randomly stimuli with changed orientation were added without the observers' knowledge. To avoid the learning process, not more than fifteen stimuli of each varied orientation were presented. A summary confusion matrix was obtained for six observers. This matrix was compared with a model matrix of distances, calculated as differences of the Fourier transforms of the objects under conditions of overlap of centroids. (The model was described in detail by Vol et al, 1991 *Perception & Psychophysics* 47 12–21). A good correlation of matrices was obtained. This result shows that the recognition process may be described with the help of this model and that there is no mechanism of invariant form recognition under conditions of angular rotation and brief exposure. The experimental data obtained about limits of invariant form recognition with angular rotation agree well with the width of orientation tuning of the receptive fields of the striate cortex.

◆ **Investigation of segmentation conditions of visual objects**

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Two psychophysical experiments were done for the evaluation of holistic pattern perception. Stimuli were fifteen Chinese characters which had no meaning for the observers. In experiment 1 the observers were asked whether they perceived each object as a whole or wanted to divide it into component parts, in which case they had to indicate these parts. It appears that practically all observers perceived as whole the objects that had no gaps. However, it may be a case of unity of separate unconnected elements, under the conditions of unshaped separate details or emphasised lines. The orientation and width of lines must be in agreement with those of other parts of the object.

In experiment 2 the minimum angular sizes for segmentation of figures were measured. The experiment was carried out with only seven hieroglyphics, which practically all observers divided into parts. It was shown that the mean size for separation of the object into two parts was 38.7 min arc, and into three parts 68.3 min arc; the widths of divided lines were 2.5–3.2 min arc. These sizes exceed the minimal sizes of clear vision by more than twice and the size of each part is equal to approximately a size of foveola. The data are discussed in terms of the analysis of image scenes and show the role of the foveola in segmentation. The hypothesis about the role of the foveola in this process was proposed by Campbell et al (1992 *Ophthalmic and Physiological Optics* 12 101).

◆ **Shape-recognition thresholds as a function of spatial filtering**

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For stimuli with central symmetry and of equal shortest linear dimension, shape-perception thresholds were found to be about the same (Gutasukas et al, 1993 *Perception* 22 Supplement, 99). The regularity depended neither on colour, nor on size, nor on spatial orientation of the stimuli. In the present study we have checked this result with stimuli different in shape, in area, and in linear dimensions. Ellipses, rectangles, and isosceles triangles were generated on the screen of an optical stimulator. Shape thresholds of the three geometrical figures were equal only in the case when both the shortest and the longest linear dimensions of different stimuli were the same. Thresholds were different for stimuli equal in area or in one of the two dimensions. If area was fixed, triangles had the lowest and rectangles the highest shape-threshold values. The data support the idea that spatial filtering plays an essential role in perceptual processes and mediates the thresholds of their mechanisms. The region of the two-dimensional spectrum limited by the fourth harmonic frequencies in several orientations is found to be sufficient for a tolerable description of the stimuli. The fourth harmonic frequency and shape threshold seem

to be interrelated values. The fourth harmonics coincide if the height and width of ellipses, rectangles, and triangles are equal. If the areas are equal, the harmonics have the lowest value for triangles, higher ones for ellipses, and the highest for rectangles. We conclude that the fourth harmonics might be used as a shape-threshold index. We propose that the processes of shape identification and discrimination are based on processing of information restricted to the range between basic and fourth harmonic frequencies.

◆ **The effect of symmetry in the tasks of detection and pattern recognition**

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The object of the study was investigation of the detection of symmetry as a shape property of the global image and comparison of the obtained results with the previous data (Gurčinionė et al, 1991 *Perception* **20** Supplement, 124) from an investigation of the effect of symmetry on pattern-recognition accuracy. In this way we hoped to clear up the quantitative and qualitative differences between symmetry detection and recognition of symmetrical and asymmetrical patterns. A backward-masking technique was used in tachistoscopic experiments on human subjects. The masking pattern was a rectangular frame formed of twelve vertical–horizontal line segments of equal length. The test patterns were the joined parts of the frame, consisting of different number of line segments. Twelve sets of test patterns were used—asymmetrical patterns, vertically symmetrical patterns, and horizontally symmetrical patterns, consisting of four, six, seven, and eight line segments. The naive observers were required to detect the kind of symmetry or its absence (ie the presence of an asymmetrical pattern). The test pattern was presented for 10 ms, the mask for 500 ms, and the interstimulus interval was individual for each subject (to reach a recognition accuracy of 50%–90%).

We found (i) the detection accuracy of vertical symmetry and asymmetrical patterns (absence of symmetry) was more or less the same and much higher than the detection accuracy of horizontal symmetry; (ii) the performance accuracy was higher for asymmetrical patterns in both tasks (symmetry detection and pattern-recognition tasks) in the case of patterns consisting of the smaller number of elements, whereas, in the case of the presentation of more complex patterns, the performance accuracy was higher for vertically symmetrical patterns in both tasks; (iii) pattern-analysis time was no shorter for symmetry detection than it was for pattern shape recognition. These results also lead us to suppose that symmetry as a property of global shape is not perceived earlier than the complete perception of the local-element structure of image.

◆ **Similarity: its definition and effect on the recognition of visual patterns**

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The similarity of patterns is an important problem in visual psychophysics. Backward masking was used in research into the influence of similarity of patterns on recognition accuracy in tachistoscopic experiments on human subjects. A rectangular frame of twelve line segments of equal length was used as a masking pattern. The test patterns, which were nonverbal figures, were the joined parts of the masking pattern. Three pattern sets (four patterns in each) with different degrees of similarity were used in the experiments. The degree of similarity of each pattern set was determined by the number of coincident line segments in the patterns being compared. The test pattern was presented for 10 ms, followed by the masking pattern for 500 ms. The interstimulus interval was individual for each subject, as the shortest interval permitting a recognition accuracy of 50%–90%. Altogether 480 test patterns (160 from each pattern set) were presented to the subject in each experiment, different sets of test patterns being presented separately. The task for the subjects was to reproduce the test patterns by drawing them. Each subject took part in seven or eight experiments.

We found the patterns with the middle degree of similarity were recognised most accurately, ie the dependence of pattern-recognition accuracy on their similarity had an inverted-U-shaped form. The results show the existence of an optimal degree of pattern overlap at which the probability of recognition is the greatest; it diminishes with the increase or with the decrease of the degree of overlapping. We propose a model of an active recognition system that can explain the effect obtained.

◆ **Stereoscopic perception of objects placed in space at will**

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It is not yet clear how the parts of objects whose distance from the observer changes gradually are perceived. These mechanisms seem more complicated than those proposed by Julesz for frontoparallel parts of objects (Julesz and Chang, 1976 *Biological Cybernetics* **22** 107–120).

Stereograms composed of dots, lines, or symbols, completely lacking monocular cues for perception were used in our experiments. With line stereograms composed of occluded line segments there is the possibility of studying perception without complex processes of form (pattern) recognition.

We measured reaction time for recognition of various stereo figures—ramps with different inclination to the background, stairs with different step numbers, and dome-like figures. The results revealed that the recognition time for the line stereograms (unlike for dotted ones) is not practically related to the inclination of the ramps. While ramp inclination changed from 22° to 44° the recognition time increased from 811 ± 27 to 2093 ± 145 ms for the dot stereograms and from 671 ± 23 to 843 ± 43 ms for the lines. At the same time our results showed the importance of vertical disparity for the perception of the line stereogram.

The experimental data allowed us to formulate a hypothesis concerning the main problem of stereo vision, that is, the problem of the identification of the pairs of fragments. We suggest a 'stripped' mechanism of identification, based on the extreme coordinates of the correspondence of pairs of fragments.

The general scheme of the stereoscopic perception is realised in a computer program. It involves the following stages: exposure of fragments, identification of pairs of fragments, determination of horizontal disparity, and calculation of the distances to figure elements.

It has been also exposed that the 'stripped' identification mechanism is highly significant for diagnosis, prognosis, and treatment of different forms of children's squint.

◆ A correlation-type computational model for control of convergent eye movement and for solving the stereo-matching problem

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A computational model and a computer simulation for solving the stereo-matching problem by vergence control is presented. (How does vergence control work, so that the same three-dimensional point will always be projected in both foveas?) The basis of the mathematical model is a $Q(h, v)$ correlation measure between the left and right images, with a central-symmetric hyperbolic weighting function $w(x, y) = (x^2 + y^2)^{-1/2}$ around the model foveas. The convergence is to the right when the following function is minimised:

$$Q(h, v) = \iint_{\text{retina}} |L(x, y) - R(x - h, y - v)| w(x, y) dx dy,$$

where h and v are the degrees of horizontal and vertical convergence, respectively, and $L()$ and $R()$ are the intensity distribution on the left and right retinas, respectively. The fixation point is on the left fovea.

The main result is that the perennial problem with stereo algorithms for area correlation is avoided by applying the hyperbolic weighting function. Therefore it is not necessary to adjust the window size—this parameter is constant and the window is equal to the model retina. (For comparison see Zheng et al, 1989 *Proceedings of the Fifth Alvey Conference* pp 91–96).

The computer simulation was tested with real colour photographs and also with computer-generated random-dot stereograms. The window size used was 250×250 pixels in all cases. When an arbitrary point in the left image is fixed, then the $Q(h, v)$ function has only one local minimum corresponding to right convergence in most cases. In complex cases (ie in multiple stable random-dot stereograms) there are more local minimums, although each corresponds to a true depth. The model explains depth perception in real colour images, single and multiple stable random-dot stereograms, double nail-illusion and 'no-man's-land'. The computer simulation shows that the model is functioning efficiently.

◆ Magnitude of perceived depth of stereokinetic cone as a function of absolute distance and eccentricity

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We measured magnitudes of apparent depth of stimuli (rotating eccentric circles with seven white and black bands) as a function of the viewing distance and the eccentricity of the smallest circle from the centre of rotation in two conditions. In the distal-size-constant condition, the diameter of the largest circle of the stimulus was 10.5 cm, and the eccentricities were 0.15, 0.9, and 2.7 cm. In the proximal-size-constant condition, the retinal size and eccentricities of the stimuli used in the distal constant condition were kept constant, irrespective of the viewing distances (0.5, 1.0, 2.0, and 4.0 m). Five subjects, assigned to each viewing distance condition,

viewed monocularly each stimulus and were asked to reproduce the apparent depth of the stimulus. The result showed that the mean magnitude of the perceived depth increased as the viewing distance and eccentricity increased in either condition. The rate of increment was larger in the proximal-constant condition than that in the distal-constant condition. The result suggests that the visual system calibrates relative motion between the smallest circle and the largest circle of the rotating stimulus according to absolute-distance information in processing stereokinetic depth.

◆ **Study of a phenomenon of visual shape degradation in low-contrast objects**

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A discernment threshold of object boundaries of complex shapes was studied, experimentally and by modelling, as a function of local curvature and size of neighbouring areas. It was found that the discernment threshold for a boundary area corresponds to a detection threshold of a simple-shaped spot (eg an oval) of a maximum size, geometrically inscribed into an object so that the spot boundaries coincide with the given boundary area. For theoretical interpretation of the obtained results, a multichannel threshold model of visual detection of brightness edges was taken which represents the Piper law (of incomplete spatial summation). It is stated that the model can be successfully employed to define a threshold contrast for discernment of the object boundary of a complex shape with the local curvature of a boundary taken into consideration. The model represents the phenomenon of shape degradation of a visual object under decreasing contrast as well as under the occurrence of noise in the image. In the context of the image-processing algorithm of the model the possibility was found of increasing the shape-discerning capability for low-contrast images. Additional experiments showed the possibility of counter-measures to resist a shape degradation and to increase its immunity to noise up to tenfold.

◆ **Categorization of surface-texture terms**

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Surface texture is an important visual cue which enables us to distinguish objects. However, its properties are not as well understood as other cues such as color. We present the results of an experiment on the categorization of texture words in the English language. The goal was to determine whether there is a common basis for the grouping of words related to surface texture, and, if so, to identify the underlying dimensions used to categorize those words. Since there is no standardized lexicon of words related to surface texture, our first task was to create a comprehensive list of such words. We used on-line dictionary-searching techniques to create a list of approximately 400 texture words in the English language. We used the 98 most-frequently occurring words from this list in our study. The experiment was carried out over a set of forty subjects. Each subject was asked to place these words into as many categories as desired on the basis of the similarity of the imagined surfaces that the words conjured up for them. We collected data from such an unsupervised classification and used it to construct a pooled similarity matrix. This matrix was then subject to the techniques of hierarchical cluster analysis and multidimensional scaling. These techniques are well suited to handling such nonmetric data.

Eleven major clusters were identified, ranging from 'random' to 'repetitive'. These clusters remained basically intact in the multidimensional-scaling solution. The stress for a three-dimensional solution obtained through multidimensional scaling was 0.18, meaning that 82% of the variance in the data is explained through the use of three dimensions. We displayed the texture terms in three dimensions, and interpreted the (rotated) axes. It appears that the major dimensions of texture descriptors are repetitive versus nonrepetitive, linearly oriented versus circularly oriented, and simple versus complex. The results of our experiment show that, despite the tremendous variety in the words we have to describe textures, there is marked similarity in the way users categorize them. This suggests that subject may possess tacit knowledge of semantic principles of organization for textures. However, there is wider variation in subjects' grouping of texture words as compared with grouping of texture pictures, as shown in our previous study.

◆ **Binocular visual direction in complex images**

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It is generally accepted that human perception of binocular visual direction is based on the concept of the cyclopean eye. Theoretical inspection of the rules of cyclopean visual direction shows a paradox for the binocular visual directions of complex stimuli in which objects partly occlude each other. We investigated how the rules of cyclopean direction are violated during viewing of structured random-dot stereograms with different depth planes. The directions of monocular and binocular visual elements were determined in an alignment task. Subjects aligned a monocular/binocular slider with a monocular/binocular test line presented in the random-dot stereograms. Stimulus conditions, in which either one line was presented in one eye and the other line in the other eye or one line was presented in one eye and the other line in two eyes, provided a critical test for validity of the cyclopean rules. The results show that the rules of cyclopean direction fail to predict alignment in these conditions. Inspection of the data shows that binocular alignment is achieved by alignment of two monocular lines presented in a single eye. Comparison of widths of monocular and binocular image parts shows that binocular elements are horizontally compressed when they are flanked by structured monocular elements. We conclude that binocular visual directions are affected by the structure of the image and cannot fully be described by geometric rules.

◆ **Attentional shift in three-dimensional space for moving observers**

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Shift of attention in depth was examined by means of a tunnel simulator. The simulator was 1/50 scale with length 13 m, and subjects could move as if really driving at various speeds in the tunnel. The task for subjects was judgment of the relative distance of targets—farther, nearer, or the same, in comparison with a fixation point. Reaction times were measured. A fixation point was presented at an apparent distance of 30 m (real-sight distance of 1.2 m) from the subjects. Targets were presented on the central line of sight at five apparent distances, from 7.5 m to 115 m (real-sight distances of 0.3 m to 2.3 m). These distances were counterbalanced on the basis both of apparent distance and of actual diopters. The brightness of targets at all distances was the same. There were two conditions. In one, subjects moved at apparent speeds of 40 km h⁻¹ or 80 km h⁻¹, or were stationary. The other condition involved the expected location of appearance of the target relative to the fixation point—valid, invalid, or neutral.

The results clearly showed that reaction times for nearer targets are shorter than those for farther targets in all conditions. This supports a viewer-centered representation of three-dimensional space. Concerning the mode of shift of attention, reaction time for shift of attention from far locations to near locations is shorter than for the reverse. This difference is largest in the high-speed condition. These results are ecologically valid. Possible underlying mechanisms are discussed.

◆ **Active texture processing**

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The role of texture processing within the overall structure of visual processing is considered. Obviously, texture serves to support many primary visual measurements, such as motion and stereopsis, which are much improved for textured surfaces. Also, texture variations can provide cues for judgments of surface shape and orientation. Last, texture can, sometimes, provide information to allow the categorisation of surfaces. A different type of function for texture is explored. It is proposed that texture serves as a preprocessing stage that can be used to identify regions of the image and regions of spatial scale/orientation that are especially worthy of immediate further processing. This is given a computational expression and applied to various sets of natural images. The results indicate that texture processing of several different types can serve a very useful function in guiding attentional visual processing.

EARLY VISUAL PROCESSING II

◆ **Tolerance to defocus, contrast, and visual acuity: a geometric model**

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A defocused letter with a contrast (C) of 1 can be recognised at a distance (threshold recognition distance) at which the ratio between its pseudoimage (η) and the confusion circle (ξ)

corresponding to any point of the letter at this distance reaches a minimum value. This ratio, η/ξ , represents the sharpness of the retinal image in a purely geometrical treatment of the image formation, providing a geometric criterion for recognition.

We repeated this classical experiment (with $C = 1$) extending it to contrasts between $C = 1$ and $C = 0.1$. Our results show that, when $C = 1$, the threshold recognition distance is such that, at least, $\eta/\xi = 2$, in agreement with previous experiments. Defocus corresponding to this distance is 4.35 D. This value is, however, slightly different for each letter, which allows us to classify them into three groups according to the degree of difficulty of recognition. In addition, our results show that, when contrast decreases, the threshold recognition distance also decreases, in such a way that the sharpness at threshold recognition distance increases linearly with C . This fact suggests that the same recognition criterion used when $C = 1$ can also be used at any contrast (at least if contrast is higher than 0.1 and defocus is higher than 1 D). On this basis, a purely geometrical model for recognition is proposed, predicting hyperbolic links (1) between acuity and tolerance to defocus at a constant contrast (including the well-known relationship between acuity and defocus when contrast is unity); (2) between acuity and contrast at a constant defocus; and (3) between tolerance to defocus and contrast in order to reach a given value of visual acuity.

◆ **Simple geometric model of a visual receptive field revealing the orientation-tuning properties of cortical neurons**

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The computer model that has been developed enables the understanding of some characteristics of orientation tuning of cortical neurons in relation to the preset parameters of receptive fields (RFs). Model RFs consist of several (up to ten) possibly overlapping excitatory and inhibitory zones. Each zone and stimulus is represented by a rectangle with a variable position, height, and width. The weight of each zone can be varied also. The stimulus (an elongated bar) can be rotated around its centre in steps of 22.5° in the range $0^\circ - 180^\circ$.

The program computes the weighted algebraic sum of areas (numbers of pixels) in overlapping regions of stimulus and RF for any given configuration of the RF, and displays the resulting polar graphs of orientation tuning (separately for excitatory and inhibitory zones and their difference). We tested several simple and complex types of striate RF, including those with end and side inhibition, RFs with several parallel excitatory and inhibitory zones, and RFs with and without overlapping zones. The dependence of orientation tuning width on the geometrical RF parameters, the size and location of the stimulus in the RF, as well as some bimodal orientation tuning were revealed by this simulation.

◆ **Superposition methods revised**

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The shape of contrast interrelationship functions (CIFs) is of particular interest in superposition experiments because of its decisive value for the class of models applicable to the data; within the class of linear systems, linear CIFs imply detection by a single linear channel, whereas curved CIFs indicate detection by probability summation between at least two channels. In the experiments on the detection of spatially modulated compound patterns reported until now, a striking link between methods and results can be found; experimenters reporting curved CIFs (eg Logvinenko, 1992 *Biological Cybernetics* 70 55-64) used the contrast-coupling technique $p(x) = m[s_1(x) + ks_2(x)]$, whereas experimenters who found linear CIFs (eg Kulikowski and King-Smith, 1973 *Vision Research* 13 1455-1478) manipulated the contrast of a test pattern superimposed on a background pattern of fixed contrast m : $p(x) = \phi(m)s_1(x) + ms_2(x)$. With the latter technique, a complete CIF (with data points ranging from the threshold contrast of the first pattern to the threshold contrast of the second pattern) cannot be obtained since the background pattern becomes suprathreshold by chance if its contrast is set to values too close to its individual threshold, although simulations of psychometric functions representing the conditional probabilities of detection yield the same pairs of threshold contrasts for both superposition methods (but show very different slopes), independent of the mathematical model used. For comparability with the CIF recorded with the contrast-coupling technique, the order of superposition must be reversed (the former background pattern must be made the new foreground pattern and vice versa). If this is done, observed CIFs show curvature when recorded with the contrast-coupling technique and consist of two linear segments when recorded with the constant-background technique, indicating that temporal adaptation occurs in spatial-superposition experiments when the contrast of a pattern does not change during a threshold determination.

◆ **Can sensory states really be ordered within a threshold zone?**

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An application of signal-detection theory to psychophysics suggests an ability in an observer to order sensory states. For instance, the rating method of determination of d' implies that observers can rank their sensory states. However, a direct test of this crucial assumption has never been conducted. If any order on sensory states exists, it induces an order on stimuli. Since an essential feature of any order is its transitivity, it means that an observer has to be able to introduce a transitive order on stimuli within a threshold zone. An experimental test of transitivity is complicated by the facts that, first, sensory states are not observable, and, second, they are stochastically related to subthreshold stimuli. Although there are several definitions of stochastic transitivity, none of them can be relevant here because even the strongest of them, $P\{s_2 > s_3\} \geq \max\{P\{s_1 > s_2\}, P\{s_2 > s_3\}\}$ for each stimulus s_1, s_2 , and s_3 , is trivially satisfied provided a monotonic psychometric function is assumed. We propose rather a different definition. An order $>$ on a set of stimuli S is transitive if for $\forall s_1, s_2, s_3 \in S$ the following strict inequality for conditional probabilities holds:

$$P\{(s_1 > s_3)|(s_1 > s_2) \cap (s_2 > s_3)\} > \max\{P\{(s_1 > s_3)|s_1 > s_2\}, P\{(s_1 > s_3)|s_2 > s_3\}\}.$$

An experiment was designed to find out whether transitivity thus defined exists for the comparison of perceived numerosity of random-dot patterns. During one session four circles (each with diameter 56 min) filled in randomly with 100, 103, 106, and 109 dots were presented simultaneously on a monitor screen. Six different pairs of circles—one per trial—were singled out in random order and the task of observers was to estimate which member of the pair contained more dots. Four hundred sessions were carried out for each of three observers. The probability of correct responses was no more than 70%, ie the differences in the number of dots does not achieve the difference threshold for perceived numerosity. Nevertheless, the conditional probability in the left-hand side of the inequality above was significantly ($p < 0.001$) greater than either of the two conditional probabilities in the right-hand side of the inequality. Hence, the pair comparisons between subthreshold stimuli exhibit a transitivity that suggests ordering of sensory states within a threshold zone.

◆ **Visual discrimination: a statistical analysis of subject's behaviour**

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In investigations of the visual system based on measurement of thresholds a subject's performance is assumed to be characterised by several basic properties—local stability ('stationarity'), statistical independence of the subject's responses from each other and from the preceding stimuli, etc. The commonly used practice is to take these assumptions for granted. Our purpose is to test them by using an appropriate statistical technique that does not depend on a particular form of psychometric function. For each stimulus level the data to be analysed are the counts that represent the numbers of a subject's different responses (first variable) classified into several groups according to conditions of stimulus presentation (second variable). These counts are accumulated in a two-entry contingency table. Then the chi-squared statistic is useful for determining whether a relationship exists between the variables. For examination of psychometric functions measured at several stimulus levels the additivity of chi-squared distribution permits the use of the sum of these individual statistics as an overall measure of independence for a set of two-entry tables as a whole. This technique was employed to test the results of experiments on the discrimination of line length. Two lines were presented simultaneously on the monitor. The psychometric function was measured with the method of constant stimuli with a "yes-no" procedure and a two-alternative forced choice. The results were obtained from eighty-five inexperienced students.

We tested whether the subject's responses were dependent (1) on the stimuli presented (ie we had to identify subjects who were insensitive or inattentive to stimuli); (2) on the experimental session (ie whether the psychometric functions obtained in different sessions could be considered statistically identical); (3) on the preceding stimuli; and (4) on the preceding responses. According to our findings, at least one of the assumptions mentioned above is not supported for considerable proportion of subjects (about 20%). When reliable methods of threshold measurement are developed, allowance must be made for this fact.

◆ **Spatial-frequency masking by noise: a model for the distribution over different spatial frequencies**

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In 1972 Stromeyer and Julesz published a paper (*Journal of the Optical Society of America* **62** 1221–1232), in which they gave measurement results of the threshold elevation of grating patterns of different spatial frequencies in the presence of one-dimensional dynamic noise. From their measurements it appears that noise in a limited spatial-frequency band also causes threshold elevation of spatial frequencies outside this band. In a previous paper (Barten, 1991 *Proceedings of SPIE* **1453** 2–15) I described a calculation method for the effect of different types of noise (eg one-dimensional static noise, two-dimensional static noise, one-dimensional dynamic noise, and two-dimensional dynamic noise) on the threshold elevation of sinusoidal luminance patterns and compared the results with measurements published in the literature. However, the use of this method is restricted to white noise of a large bandwidth and to luminance patterns with a spatial frequency within the range of the noise band.

I now generalise my calculation method to a model that also takes into account the effect of noise on spatial frequencies outside the noise band. For this purpose, a distribution function is introduced for the spread of the effect over spatial frequencies. The chosen form of this function is largely based on the measurement by Stromeyer and Julesz. The calculation results appear to be in very good agreement with these measurements. The model predicts a decrease of the masking effect with 9 dB octave⁻¹ in the direction of lower spatial frequencies and with 15 dB octave⁻¹ in the direction of higher spatial frequencies. This means that noise generated in a limited frequency band is generally more disturbing at lower spatial frequencies than at higher spatial frequencies. The model can be of importance for the prediction of masking effects caused by the spatial sampling which is applied in modern displays.

MOTION PERCEPTION

◆ **Deconfounding contrast and speed: contrast normalisation or ratio models?**

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When two gratings moving at the same speed are presented simultaneously, the lower-contrast grating appears slower and the higher-contrast grating appears faster than their physical speeds (Stone and Thompson, 1992 *Visual Research* **32** 1535–1549). Stone and Thompson suggested that this phenomenon is caused by contrast normalisation, and that local motion energy is divided by average contrast to compute speed independently of contrast. An alternative would be to compute speed from the ratios of the outputs of spatiotemporal filters tuned to different velocities (Adelson and Bergen, 1985 *Journal of the Optical Society of America A* **2** 284–299). One way of distinguishing between contrast-normalisation and ratio models is to see whether the speed or temporal frequency of the high-contrast grating influences the perceived speed of the low-contrast grating. A contrast-normalisation model would predict the same slowing in perceived speed of the low-contrast grating (because of overcompensation for contrast) regardless of the temporal properties of the high-contrast grating. A ratio-speed model would predict that the perceived speed of the low-contrast grating should be biased towards the speed of the high-contrast grating because the high-contrast grating affects the activity of mechanisms tuned to different velocities.

We measured the effect of the presence of high-contrast flicker at different temporal frequencies upon the perceived speed of 1 cycle deg⁻¹ gratings of contrast 0.02, moving at 6 deg s⁻¹. Flicker at a temporal frequency lower than the low-contrast moving grating decreases its perceived speed while higher-temporal-frequency flicker increases its perceived speed. This is consistent with a ratio model.

◆ **Propagation of local motion correspondence**

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I examined how the direction of apparent motion in one part of a scene can propagate and constrain motion direction in another part. The stimulus scene consisted of an array of dots moving in the same physical direction at the same time. According to the proximity rule, the dots in the interior of the array should appear to move rightward and the dots at the edges should appear to oscillate horizontally. However, I found that (1) with long frame durations, the interior dots also appeared to oscillate; (2) with shorter frame durations, the likelihood that the

subjects perceived rightward motion at the center of the array increased; (3) oscillation was observed at the edges regardless of frame durations; (4) when opaque objects were placed on both the left and the right sides of the array as occluders, only rightward motion was observed in the center and at the edges of the occluders independently of frame durations; (5) in all of these cases, basically similar results were obtained with both foveal and peripheral viewing of either the center or the edge; (6) with longer frame durations, the interior area within which oscillation was observed became larger; and (7) with increasing total duration of the moving array, the probability of observing oscillations in the center became higher. These findings suggest that signals for motion correspondence (oscillation) can gradually propagate to distant units. This can be explained by a locally connected iterative network model.

◆ **The mechanism underlying the detection of non-Fourier motion is tuned to velocity and not temporal frequency**

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Contrast thresholds were measured for direction discrimination by means of a two-alternative forced-choice procedure with a method of constant stimuli. The stimulus was composed of Gabor micropatterns pseudorandomly positioned in a row either above or below a fixation mark at an eccentricity of 0.5 deg. The Gabor micropatterns were presented for 560 ms and two types of motion were used, Fourier motion and non-Fourier motion. In the Fourier-motion condition the Gabor micropatterns were displaced by rapid steps of a quarter of the wavelength (λ) of the cosine component of the Gabor. In the non-Fourier-motion conditions the envelope of the Gabor micropattern was displaced whilst the cosine component remained stationary. Thresholds for direction discrimination were measured for both types of motion for a range of velocities ($\geq 1 \text{ deg s}^{-1}$), spatial frequencies ($\lambda = 0.05, 0.1, 0.15 \text{ deg}$), Gabor envelope sizes (σ), and micropattern densities (N).

Under the above conditions, direction-discrimination thresholds for Fourier motion show low-pass tuning functions with respect to velocity, with log sensitivity decreasing at different rates for different values of λ . These functions become parallel when plotted in terms of temporal frequency. Thresholds are unaffected by variations in σ and N . Direction-discrimination thresholds for non-Fourier motion show band-pass tuning with respect to velocity. Variations in λ or N serve to change the level of sensitivity but not the position of the tuning function. For higher velocities ($> 2 \text{ deg s}^{-1}$) the rate of reduction in log sensitivity is the same when plotted as a function of velocity (for all conditions tested) but different as a function of temporal frequency (ie the temporal frequency of the stimulus envelope—the spatial wavelength of the stimulus envelope equals the average spacing of the Gabor micropatterns). Fourier motion is detected by a set of mechanisms tuned to temporal frequency, whereas the mechanisms that underlie the detection of non-Fourier motion are tuned for the velocity of the stimulus envelope and not its temporal frequency.

◆ **Perceived object motion in depth during simulated ego-motion**

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When referring to the velocity of an object, we usually mean its velocity relative to the static surroundings. Our previous studies with simulated ego-motion could be interpreted as evidence that we judge object motion relative to the environment, accounting for our own motion on the basis of visual information. However, we proposed that we perceive object motion relative to ourselves, visual information only being used to account for our rotations. If so, changes in the distance of a target during simulated ego-motion in depth should be attributed to the target moving in depth. In the present study, subjects looked into a 'box' (40 cm \times 40 cm \times 120 cm) with eight squares at random positions on the far surface, and a regular pattern of stripes on all other surfaces. LCD shutter spectacles were used to present the image on the computer screen in stereoscopic depth. A 'cube' appeared at 70–80 cm from the observers, approaching them at 20 cm s^{-1} . Once the cube was 60 cm from the observer, the image on the screen started changing to simulate motion of the observer in depth. At the same time, the velocity of the cube changed. The simulation continued for another 500–1000 ms. Subjects were asked to report whether the cube moved faster, at the same speed, or more slowly during the simulated ego-motion. They reported that the target continued to move at the same speed whenever its simulated velocity relative to themselves was unaltered. Our instructions may have stimulated subjects to report on motion relative to themselves. We therefore showed subjects how they had performed, and repeated the experiment after specifically instructing them to report on motion

relative to the surrounding. Subjects still did not account for their own motion, but the variability in their responses increased tremendously. This supports the assertion that we only use visual information to account for our own rotations.

◆ **Model of local velocity in primary visual cortical cells**

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A motion model for the early stages of motion processing in the visual cortex which focuses upon velocity properties is presented. The model presents analytically the correlation between the velocity-tuning curve and various parameters of the cell. The 'building block' for this model is the 'rebound response', which is the excitatory response evoked when a sufficient inhibitory stimulus is turned off. This response enables detection of spatial and temporal edges. The model suggests that adjacent subunits in the primary cortical cells have different weight functions in their rebound responses, and thus a synergistic response is evoked in the preferred direction (Spitzer et al, 1994 *Spatial Vision* in press). The analysis deals separately with the two cutoff points of the velocity-tuning curves. The model predicts a linear relation between the low cutoff point and the integration time, and an inverse correlation with the receptive-field size. The high cutoff point is inversely correlated with the cell threshold. Simulation analysis enabled us to find further correlations. These results of the model were simulated by means of physiological parameters, and good agreement was found with physiological findings.

◆ **Relative contribution of luminance and colour to motion processing assessed by steady-state evoked potentials**

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Many psychophysical experiments have shown that both luminance and colour contribute to motion perception. The aim in the present study was to compare the activities evoked by chromatic-carried and luminance-carried motion, and test their interaction. The stimuli were vertical square gratings of 1 cycle deg^{-1} , moving alternately from right to left at a velocity of 15 deg s^{-1} . Motion-related VEPs (see Wattam-Bell, 1991 *Vision Research* 31 287-297) were recorded for 'pure' luminance stimuli and for stimuli where the luminance and colour components were either drifting along the same direction ('plus' stimulus) or pitted against each other ('against' stimulus). The chromatic contrast was fixed (full red/green modulation). The equivalent luminance contrast (EqLC) was assessed psychophysically for each observer by the motion-cancellation technique ('against' stimulus). The contrast of the luminance component was then varied as a ratio of the EqLC.

The amplitude of the motion-related VEPs obtained with the 'pure' luminance stimulus increased linearly with the logarithm of the luminance contrast. This relationship and the slope of the function were preserved for the 'plus' stimulus. The latter function yielded, however, a vertical shift which was larger than expected from the linear summation of the chromatic contrast as estimated by its EqLC. For the 'against' stimulus, the amplitude of the VEPs displayed a nonmonotonic function of the luminance contrast. A minimum but not null amplitude was observed for a luminance contrast equal to the EqLC of the chromatic component. This residual component was not expected, given the ambiguous motion perception obtained under identical conditions. Taken together, the data suggest that, at an unspecified processing stage, chromatic and luminance components that drift add algebraically but that the summation coefficient depends on whether the two components share the same direction or are pitted against each other.

◆ **Trade-off between speed and position and speed and orientation in motion processing**

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According to the uncertainty principle the accuracy in estimating speed and position cannot be simultaneously arbitrarily high. How does the visual system deal with this inescapable trade-off? The question has been addressed by means of a double-task experiment whereby the observer was asked to estimate both the speed of a drifting line and the position of a briefly flashed line relative to the drifting one (dynamic vernier). As a control experiment, the briefly flashed line was oblique and the observer was asked to estimate its orientation—SO condition.

When compared with single-task experiments, double-task performances show a significant impairment in speed discrimination when coupled with either position or orientation judgments. Orientation discrimination also deteriorated when assessed in the SO double task. Position (or vernier) judgments, on the other hand, do not depend on whether they are measured in single or double tasks. Performances on one task do not depend on the difficulty of the other task.

Finally, the conditional probabilities *Correct[task 1]-given-Correct[task 2]* and *Correct[task 1]-given-Wrong[task 2]* do not differ significantly.

The data are consistent with the idea that a spatiotemporally oriented (motion) sensor provides simultaneous information on speed, position, and orientation. The asymmetry of the speed-position trade-off may be accounted for in terms of a limitation in spatial (and temporal) pooling whereby the system optimises dynamic acuity at the expense of speed discrimination. Attending to a motion sensor whose spatial orientation is intermediate between the orientations of the moving target and of the slanted probe would account for the balanced drop in speed and orientation performances in the SO condition.

◆ **Reaction time to onset of accelerated visual motion**

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In our first experiment a random-dot pattern appeared on a screen and, after a random period, started to move within a stationary circular area (diameter 8.9 deg, fixed 4.5 deg above the fixation point) with a constant acceleration. The subject's task was to press a button as quickly as possible after detecting the motion. The reaction time (T) was measured. Accelerations (A) of 1.5, 3.1, 6.2, 12.5, 25, 50, and 100 deg s⁻² were employed. T decreased with increasing acceleration. The best fit of the relationship between T in seconds and A in deg s⁻² for the data of six subjects was obtained by a power function, $T = 0.422A^{-0.375} + 0.223$. Three hypotheses that predict power functions with different exponents are considered. (1) The reaction is elicited when the motion reaches a critical velocity. This hypothesis predicts an exponent of -1 , and is not supported by the results. (2) The reaction is elicited after a constant displacement of the dot pattern. The predicted exponent is -0.5 , which approximates that found in the experiment. (3) The reaction is elicited when the running variance of the positions that the stimulus passes during the motion exceeds a critical value (Dzafarov et al, 1993 *Perception & Psychophysics* 54 733-750). The predicted exponent of -0.4 can successfully fit the data. In another experiment we measured the reaction time to onset of motion with constant velocities (V) of 1, 2, 4, 8, and 16 deg s⁻¹. The relationship between T and V was a power function, $T = 0.137V^{-0.55} + 0.220$. This result rules out the constant-displacement hypothesis, which predicts an exponent of -1 . The model of Dzafarov et al predicts an exponent of -0.66 for this case. We conclude that this model may be successful in explaining the speed of reaction to motion onset.

◆ **Bridging the gap between plaids and random-dot kinematograms in the perception of motion direction**

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Neurons in area MT sensitive to motion direction have been studied by means of plaid patterns or random-dot kinematograms. One difference between the two patterns is that the former consist of differently oriented moving gratings, whereas the latter contain no oriented elements. We attempted to bridge the gap between these two patterns. Concurrently with the judgment by the subjects of the dominating motion direction, visual evoked potentials (VEPs) were recorded from occipital electrode positions.

In the first experiment, random-dot kinematograms contained two different motion directions; one direction was defined by 50% of the pixels moving diagonally downwards to the left, whereas the other direction, defined by the remaining 50%, was varied between 180° and 0° in five steps. The circular display was 6 deg in diameter with a central fixation point. The two different motion directions could be identified clearly for all conditions, without any impression of a global coherent motion. In the second experiment, a 'fragmented-plaid' pattern was created by substituting lines (0.24 deg) for dots (0.033 deg). In one condition 50% of the lines were oriented diagonally to the left, with the remainder orthogonally oriented. In the other, all lines were oriented diagonally to the left. Motion direction was varied as described above. Here, the impression of global coherent motion did result, but was more probable when the orientation of the lines for the two motion directions coincided. In the first experiment the amplitude of the prominent VEP negativity varied as a function of the angle between the two motion directions and was characterised by a U-shaped function with a minimum at 90°. No such relationship was found for 'fragmented plaids'. The implications of these results for current research on plaids are discussed.

◆ **Motion direction evoked potentials and ratings of global motion direction**

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Visual evoked potentials (VEPs) elicited by motion direction onset were recorded by using random-dot kinematograms in which the percentage of coherently moving pixels was varied between 20% and 80%. Velocity as well as global luminance was held constant. VEPs were recorded at seven occipital electrode positions; centred at OZ, three electrodes were fixed equidistantly and laterally over the left as well as over the right hemisphere. Simultaneously with the recording of VEPs, twelve subjects rated the perceived strength of a global motion direction on a seven-point scale.

The potentials evoked by motion direction were characterised by a negativity occurring at about 200 ms. Increasing the percentage of coherently moving pixels increased both the rated subjective strength of global motion direction and the amplitude of the negative peak monotonically. The correlation between the means of these two measures exceeded 0.9. Although the motion pattern was centred on the fovea, the negative potential was clearly lateralised; amplitudes recorded from the right hemisphere were significantly higher than those recorded at the homologous position of the left hemisphere. Furthermore, the right hemisphere was more sensitive to variation of motion-direction information, as indicated by a steeper slope of the function relating amplitude to the percentage of coherently moving pixels. These results were replicated in a second experiment with the same subjects.

Results are discussed with regard to lateralised EEG background activity as well as sex differences. The dependence both of the psychophysical judgments and of the VEP amplitudes on the percentage of coherently moving pixels parallels findings obtained with single-unit recordings in area MT.

◆ **Spatial integration of velocity signals via Markov random fields**

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In a previous paper (Gurney and Wright, 1992 *Biological Cybernetics* **68** 173–181) we showed how a two-stage neural network model could solve the aperture problem locally within a single velocity module. A further stage of processing is required in order to explain phenomena such as motion capture, coherence, segmentation, and transparency, which should involve the spatial interaction of intermodule signals. We propose a model in which velocity parameters (speed and direction) are encoded as the site values over a pair (one for each parameter) of coupled Markov random fields (MRFs). Each site therefore has a tendency to take on the same value as its neighbours, according to a pairwise Gibbs potential, and is also 'driven' by a singleton potential which reflects the motion energy from the first stage. The pairwise links allow emulation of capture and coherence while the strength of the singleton reflects the height and spread of the activation profile encoding velocity. In this way, we can model spatial differences in motion energy, as well as the extent to which the aperture problem has been solved. Transparency is modelled by using two speed and direction sites per module. MRFs have been used successfully in machine vision (Geman and Geman, 1984 *IEEE Transactions PAMI* **6** 721–741) for image restoration analogous to smoothing. However, our model has significance, not as a literal description of the animal visual system, but as a computational equivalent of a neural-level model which contains lateral, intermodule connections. We assume that such connections are concentrated between areas representing similar velocities and model this by making the pairwise potential dependent on the site-value difference. This mechanism allows for the emulation of segmentation without recourse to the special 'line processes' normally used to do this.

◆ **Phenomenology of transient motion coherence**

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We present an example of a phenomenon, previously named illusory pausing (Harris et al 1978 *Psychonomic Society*; Goldberg and Pomerantz, 1982 *Journal of Experimental Psychology* **8** 547–561), here termed transient motion coherence. Consider two identical arrays of random dots, superimposed and viewed monocularly, one array drifting to the left and the other to the right, with full wraparound. A momentary coherence of the dot planes is seen periodically, at which point the motion in the display appears to cease. Significantly, the effect is still present under small vertical offsets of one array relative to the other. This contrasts with previous findings, where the illusion requires exact dot coincidence.

Spatial similarity, such as occurs with Glass patterns [Glass, 1969 *Nature (London)* **243** 578–580], was considered to be a possible cause of the effect, since the display consists of not only a constant opponent motion, but also a regularly varying spatial similarity. To test this, we replaced the coherent rightwards and leftwards motions with a dynamic display, in which no coherent motion was visible, but in which the variable spatial similarity was preserved. Whilst a spatial regularity was still perceived, no motion coherence was visible, suggesting the phenomenon is motion based. We then varied velocity and dot density, using a method of adjustment to measure the minimum relative vertical offset required to eliminate transient motion coherence. With the more-densely populated displays (dot density 30%), the threshold for the effect was maximal at around $1-1.5 \text{ deg s}^{-1}$, with an offset of approximately 11 min arc. At lower and higher velocities, the threshold decreased to about 7 min arc. As the dot density progressively decreased, the threshold appeared to become largely independent of velocity, at about 7 min arc.

We suggest that this effect may show evidence of local motion opponency where, as two dots moving in opposite directions move close together, the overall motion signal for that region becomes zero.

◆ **Use of parallax components in manual self-motion control**

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Viewers use motion parallax in self-motion perception. In this study I tested the effects of manipulating the availability of parallax information on self-motion control. This was accomplished by orienting a camera in different ways as viewers hovering over a virtual scene used a joystick to maintain position, while being buffeted forward and back by optically simulated gusts. In experiment 1, root-mean-square position errors indicated that viewers performed better when the camera simulated pursuit fixation of a location on the ground than when it pointed toward the horizon continuously. Because simulated pursuit subtracts a global component from the optic flow field, this was interpreted as a result of the greater magnitude of parallax components, particularly divergence and deformation, that remain in the display when the camera pursues a nearby point in the scene. In experiment 2 I tested whether this gain would be influenced by the increased availability of eye-movement information when the moving camera reveals nearby terrain but does not simulate pursuit fixation. Viewers performed better when the camera pointed at a ground location 1.0 eye height ahead as opposed to 3.0 eye heights ahead. On an imaginary fore-aft axis drawn on the ground, the former location is the point at which divergence and deformation are maximal when the camera moves forward and back over flat terrain. Performance was similar between displays that simulated pursuit and those in which the orientation of the camera was fixed. This was interpreted as evidence that, under certain conditions, viewers can control their position adequately by using only projective transformations—not merely how fast elements move optically, but how their images expand, rotate, and change shape.

◆ **Motion-compensated temporal integration and the computation of motion energy**

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The best possible performance (d') in the detection/identification of a moving signal embedded in spatiotemporal Gaussian noise is achieved by an observer (ideal observer) that integrates the response of matched filters along the motion path of the signal (motion-compensated temporal integration, MCTI). Performance (d') for the ideal observer increases as the square root of the number of independent noise frames in the sequence. Human observers perform MCTI within 700–1000 ms, and with a statistical efficiency of 5%–7% (Eckstein et al, 1993 *OSA Annual Meeting Technical Digest* **16** 155). To account for the effect, we proposed a model in which the observer monitors a unit that temporally integrates the instantaneous output of a set of activated spatiotemporally oriented filters (Eckstein et al, 1993 *Perception* **22** Supplement, 93) such as those suggested for the computation of motion energy (Adelson and Bergen, 1985 *Journal of the Optical Society of America A* **2** 284–299). However, the motion system includes two additional stages—a squaring nonlinearity that computes motion energy and an opponency stage which subtracts rightward from leftward motion energy. If the temporal integration is computed after the squaring operation, then no MCTI should be observed for a phase/polarity discrimination. If the integration occurs after the opponency stage, then no MCTI should be observed across opposite motion directions. We tested these predictions by using a two-alternative forced-choice

phase discrimination of a moving Gabor patch for increasing number of frames (1, 4, 8, 20) and a four-alternative forced-choice detection of a Gabor patch moving for half of the frames in one direction and half in the opposite (20 frames in total) versus one moving 10 frames in one direction. Performance (d') improved significantly as a function of number of frames for the phase-discrimination task. In the second task, performance was significantly higher for the 20-frames condition, showing that there is MCTI across opposite directions. These results suggest that MCTI is computed before the squaring nonlinearity and opponency stages.

◆ **Discriminating rigid from nonrigid motion in the kinetic depth effect**

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Psychophysical evidence showing that the human visual system is subject to certain errors in extracting three-dimensional information from structure-from-motion displays has led some researchers to hypothesize that three-dimensional shape perceived in projections of rotating or translating objects might be affine rather than metric (Norman and Todd, 1993 *Perception & Psychophysics* 53 279–291). This hypothesis, however, is insufficient to explain the discrimination of rigid from nonrigid motion, and the perception of angular and depth magnitude in structure-from-motion displays. As an alternative, we propose that misperceptions of Euclidean shape can be accounted for in terms of an heuristic analysis based on first-order temporal relations.

Accuracy in discriminating rigid from nonrigid motion was investigated for orthographic projections of two nonparallel connected random-dot surfaces having either similar or different slants (the absolute value of the angle between surface normal and the z-axis). The two surfaces were simulated as undergoing rotations of either the same (globally rigid motion) or different (globally nonrigid motion) magnitude. The observers' task was to decide whether, during rotation, the relative inclination between the two surfaces remained constant (perceived rigid motion), or changed (perceived nonrigid motion). It was found that configurations of surfaces with similar slant were perceived veridically (globally rigid transformations were perceived as rigid and globally nonrigid transformations were perceived as nonrigid), whereas configurations of surfaces with different slants were not (globally rigid transformations were perceived as nonrigid and globally nonrigid transformations were perceived as rigid). These findings are consistent with an algorithm for recovering three-dimensional structure from two views of four points based on an heuristic procedure of minimization proposed by Koenderink and van Doorn (1991 *Journal of the Optical Society of America A* 8 377–385).

◆ **Perceived speed in contrast-modulated gratings**

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Work on the perceived direction of non-Fourier motion in a range of stimuli has been influential in the development of current theories of motion perception. A number of models propose a rectifying prefilter to account for perception of non-Fourier motion, while others seek to exploit the relationship between group velocity and amplitude velocity (Fleet and Langley, 1993 Robotics and Perception Laboratory Technical Report RPL-TR-9309, Department of Computing Science, Queen's University, Kingston, Canada). However, little empirical work has been carried out on the perceived speed of non-Fourier motion.

In this study we set out to measure psychophysically the perceived speed of the low-contrast regions of contrast-modulated gratings. Observers compared the perceived speed of a luminance sine grating and the low-contrast regions of a contrast-modulated sine grating in a two-alternative forced-choice paradigm in which the speed of the luminance grating was varied by using adaptive probit estimation to determine a psychometric function. The point of subjective equality was taken as a measure of the perceived speed of the modulation. It was found that perceived envelope speed declined as a function of the spatial frequency of the carrier grating. For all spatial frequencies perceived envelope speed decreased away from veridical as the speed of the carrier grating changed from being equal in direction and magnitude to that of the modulation, through static, to equal and opposite. It was found that this behaviour could be predicted by using a multichannel gradient model of motion perception (Johnston et al, 1992 *Proceedings of the Royal Society of London, Series B* 250 297–306). It is not yet clear that approaches based on early rectification or the measurement of group velocity are able to account for these results, and it may be that they are simply due to the operation of a robust gradient scheme not specifically geared to the perception of non-Fourier motion.

◆ **Monocular perception of change in heading direction**

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The visual motion during ego-motion depends on translation ($\bar{v}\sigma$ heading), rotation ($\bar{\omega}$ change in heading direction), and structure (E , environment, σ visible distance, and $\chi_E: R^d \rightarrow [0, 1]$ a characteristic function). The environment influences the translational component. Its familiarity might simplify the decomposition of translation and rotation. For example, heading across a plane generates visual motion that relates bijectively to two-dimensional motion. Subjects fixated monocularly in the heading direction of a simulated ego-motion through an environment represented by 500 pixels of a fixed size. They indicated the perceived sign and compared magnitudes of directional changes in heading in a two-alternative forced-choice experiment. Several environments were used, such as floors, ceilings, woods, clouds, and flat land, where motion vectors are collinear. Familiar environments are slightly advantageous (wood > ceiling). Short presentation times (1 s) suffice. Both the performance and the structure percept worsen at pixel lifetimes of less than 3 frames (13 ms per frame). Varying the field of view between 90 deg and 150 deg has little influence. Subjects actually perceive $\bar{\omega}/|\bar{v}|$, which relates to visual curvature for planar environments. The threshold level for sign discrimination of $\bar{\omega}/|\bar{v}|$ is lowest where it is 3° for heading directions in the viewing direction and grows to 15° for heading directions orthogonal to the viewing direction. For a threshold of 3° this means, for instance, that with 100 m visible distance, 1° s⁻¹ rotation is detectable at a velocity of 30 m s⁻¹, and 0.1° s⁻¹ of rotation is detectable at a velocity of 3 m s⁻¹, and with 10 m visible distance 1° s⁻¹ of rotation is detectable at a velocity of 3 m s⁻¹. The threshold levels for magnitude discrimination of $\bar{\omega}$ are high: 0.15 (bending) up to 0.3 (rolling). In flat land both the performance and the structure percept worsen at lifetimes of less than 5 frames. Magnitude discrimination thresholds are 8 times higher. Thus visual motion with varying directions determine the percept of rotation in depth faster and more robustly than do collinear visual motions.

◆ **Monocular perception of motion in depth from parallax**

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Local magnitude differences in visual motion are called parallax. In four experiments we investigated the role of parallax for the monocular perception of transparent motion in depth. With the results we constructed a simple physiological model. Depth can be perceived from a change in perspective, which from the observer's point of view always reflects a translation. Rotation about an axis not through the observer contains translation that accounts for the change in perspective. As three-dimensional motion stimuli we used moving random-dot clouds without static three-dimensional cues and without dynamic occlusion.

In experiment 1 (Donker et al, 1993 *Perception* 22 Supplement, 80) the direction of rotation of a transparent object had to be indicated with and without lateral head movements that change the parallax magnitude. Active observers could handle twice as much transparency as passive observers. In experiment 2 (De Poot et al, 1993 *Perception* 22 Supplement, 78) we compared direct and delayed (168 ms, phase-lag ≈ 0.2) feedback in the active viewing condition from experiment 1. Feedback delays do not affect the performance of most subjects, so the use of parallax magnitude is often very qualitative. This is consistent with the findings of van Damme and van de Grind (1994 *Perception* 23 Supplement, 28). In experiment 3 (Bruil et al, 1994 *Perception* 23 Supplement, 57) the direction of curvilinear self-motion had to be indicated. The saturation or depth of the parallax (ie the quotient of the maximal visible parallax and the parallax at infinite sight) determined the detection thresholds for path curvature. In experiment 4 (Fitzverploegh et al, 1994 *Perception* 23 Supplement, 59) the velocity of self-motions had to be compared. The parallax saturation affects the perception of velocity. A nonstable saturation can double the velocity-discrimination thresholds. A simple physiological model that we constructed from these results predicts the typical integration and segregation phenomena reported for detection of transparent motion.

◆ **Processing of transparent motion information in complex cells in area 17 of the cat**

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We examined directionally selective responses of complex cells in area 17 of the cat to transparently moving random pixel arrays. The use of transparent motion makes it possible to stimulate

cells with two identical patterns moving at the same time and place in different directions or at different speeds. This provides critical information on the mechanisms and interactions that underlie the directional selectivity of these complex cells. The data can also be compared with results of human psychophysical experiments performed with the same stimulus (van Wezel et al, 1993 *Perception* 22 Supplement, 79–80).

Adults cats were anaesthetised with a 70:30 mixture of $N_2O:O_2$ supplemented with 0.1%–0.4% halothane. The eyes were immobilised by administering gallamine triethiodide intravenously ($10 \text{ mg kg}^{-1} \text{ hr}^{-1}$). Moving random pixel arrays were viewed monocularly. To generate the transparent stimulus we spatially interleaved a 256×256 pixel array in such a way that half of the pixels could be moved independently from the other half. When the pixels move in different directions or at different speeds this stimulus design gives a vivid impression of two transparently moving patterns. The mean luminance of the array was 50 cd m^{-2} and the contrast was 70%. At the viewing distance of 57 cm the pixel size was $3.2 \text{ min} \times 3.2 \text{ min}$.

The response to a random pixel array in the preferred direction of a cell is reduced when a second array is transparently moving in another direction. In the condition of two oppositely moving patterns in the preferred and nonpreferred direction the reduction is maximal and typically about 50%. Speed-tuning characteristics of excitatory and inhibitory effects are equal. These results are in agreement with human psychophysical findings that two transparently moving random pixel arrays in different directions can be segregated perceptually, but that the direction of one array is harder to detect in these conditions when the speeds of the arrays are equal.

◆ **What is the relation between motion-aftereffect duration and recovery from adaptation?**

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It is generally assumed that the motion aftereffect after prolonged motion adaptation is due to fatigue of motion channels tuned to the adapting direction. The duration of the motion aftereffect is considered to be directly related to the time required for the motion channels to recover from adaptation. To test this hypothesis we compared the duration of the motion aftereffect with the time needed for recovery of direction sensitivity after motion adaptation. Direction discrimination was measured as luminance-noise thresholds for global direction discrimination in a moving random-pixel array, before adaptation and at different recovery times after adaptation. During the recovery time a stationary random pixel array was presented to monitor the duration of the illusory motion percept. For a 5 s adaptation time the motion aftereffect lasts about 2 s. However, the recovery time for motion-direction discrimination is much longer. It can take up to nearly 1 min before the noise threshold is back at the baseline performance level. Thus, the duration of the motion aftereffect is not directly related to the duration of decreased directional sensitivity.

◆ **Direct comparison of SNR-thresholds for first-order and second-order motion of lines**

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In a random pixel array (RPA) of 256 columns and 256 rows pixels are randomly assigned either the luminance value $b (=L + \Delta L)$ (bright) or $d (=L - \Delta L)$ (dark). If on frame k (frame rate 90 Hz) a given column j of pixels is refreshed, that is, given new b and d assignments, unrelated to previous assignments, and this is done for column $j + i, j + 2i, j + 3i$, etc, on frames $k + m, k + 2m, k + 3m$, etc, one sees a flickering line (F-line) move from left to right across the otherwise static array. The velocity equals i/m pixels frame⁻¹. This kind of motion is often called 'second-order'. If one moves single columns of nonrefreshed pixels *coherently* one has first-order motion of C-lines (C from 'coherent'). If C-line pixels are refreshed after every r jumps, their lifetime is $r + 1$ frames. Thus the F-line is equivalent to a C-line with a pixel lifetime of 1 frame. Moving C-lines and F-lines allow us to study coherent first-order motion with decreasing C-line pixel lifetimes, merging into second-order F-line motion at single frame lifetimes. Sensitivity of human observers was quantified with luminance signal-to-noise-ratio method. Multiple equidistant F-lines or C-lines (eg 4, 8, 16, 32 lines) or F-bars and C-bars were used, all moving with the same velocity. (A bar consists of ≥ 2 contiguous pixel columns). The dependence of C-line/bar or F-line/bar motion on the number and vertical extent of the lines/bars was studied as a function of velocity and temporal frequency. The luminance signal-to-noise-ratio threshold increases for decreasing temporal frequency in the range below about 15–20 Hz. A detailed comparison of F-line and C-line motion properties is presented, leading

to conclusions about the commonalities and differences in the corresponding second-order and first-order motion mechanisms.

◆ **Monocular perception of change in forward speed**

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The scale of the visual world is ambiguous in monocular observation. The magnitude ($|\dot{v}\sigma|$) of self-motion and the scale (σ) of the outer world can perceptually be arbitrarily assigned. We investigated human monocular perception of change in forward speed for different environments and for different temporal frequencies. As a model we consider a cognitive system that assigns magnitude to the motion percept followed by a system to monitor changes in assignment. Two Weber phenomena are predicted by this model—perception of change in forward speed qualitatively bounded by $|\Delta\dot{v}\sigma|/|\dot{v}\sigma| = |\Delta\dot{v}|/|\dot{v}|$ and quantitatively bounded by $|\Delta\dot{v}'|/|\dot{v}'|$. In four two-alternative forced-choice experiments we investigated the perception of (1) forward speed, (2) uniformity in forward speed, (3) the sign of change in forward speed, and (4) the magnitude of change in forward speed. Proportional changes in forward speed of 0.1 are detectable. The discrimination of uniform and nonuniform speed is optimal at a modulation frequency of 1 Hz. This compares well with realistic modulations in motion as occur during walking. A proportional magnitude modulation of 0.1 about a reference level is detectable. For short dot lifetimes both changing maximal visible distance and changing field of view have an inversely proportional effect on the perception of speed. For a 3 frames (13 ms per frame) lifetime the velocity discrimination threshold can double to 0.2 as a result of these environmental changes. The sign of acceleration is not very well detected if the starting speed is unknown. A proportional decrease/increase of speed by 0.3 is perceived. The perception of acceleration magnitude is poor. Only 100% differences in acceleration are detected. In the perception of change in forward speed, subjects seem to trade off between tracking of individual visual elements and environmental statistics. The percept of acceleration is very qualitative.

◆ **Head movement decreases integration time in structure from motion**

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Motion parallax is one of the many cues for the perception of three-dimensional structure. It can be generated when an object moves in front of a static observer, when a moving observer is looking at a static object, or when both are moving.

Is there any improvement of the three-dimensional percept when ego-movements are made? If so, does this nonvisual information enter the structure-from-motion pathway at the same stage as the visual (motion) information?

We addressed these questions in a curvature-discrimination experiment in which a forced choice paradigm was used. Stimuli were random-dot kinematograms with dots limited in lifetime. The kinematograms simulated cylindrical surfaces with a certain curvedness. The task was to discriminate two surfaces with different curvatures. We measured the fraction of correct responses (psychometric curves) as a function of dot lifetime. There were two conditions: (1) a static object, head movement fed back to the random-dot display by means of a movable chin-rest, and (2) a rotating object but no head movement of the observer. Lifetimes varied from 2 to 10 frames; frame duration was varied by a multiple of 16 ms. These limited-lifetime stimuli therefore selectively stimulate only bilocal motion detectors with the same delay.

The first results show that the percentage of correct responses is higher for the head-movement than for the no-head-movement condition, and the percentage of correct responses increases with lifetime in both conditions. This suggests that the structure-from-motion process needs some build-up time, which may be shortened by head movements. Possible explanations are (1) that the nonvisual information presets the starting level of the integration process for structure from motion or (2) that the nonvisual information causes the integration process to have a smaller typical time constant.

◆ **The perception of surface slant by static and by moving observers**

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The projection of objects on the retina changes when an object moves or when an observer moves. In these ways, information of three-dimensional structure can be obtained. We investigated the perception of surface slant from motion and compared performance in two conditions: (1) with head movement and a static object; and (2) no head movement, but with a moving object. In the head-movement condition, the position of the head was measured by a moveable

chin rest. In both conditions, motion parallax was the only depth cue that was available. These conditions were used in two tasks: a slant-discrimination task and a slant-categorisation task. The main question was, can head movements improve perception of surface slant? Observers looked at elliptic three-dimensional surfaces or at planar surfaces. These surfaces were defined by moving random dots on a monitor. The surfaces were slanted between 0° and 30° . The direction of the slant (tilt) could be 0° and 90° or could be randomised. Head movements had almost no effect on the perception of surface slant. The slant of flat surfaces was perceived better than the slant of curved surfaces. When the quantity of the rotation under the second condition was randomised, the slant-categorisation became more difficult in both conditions. The results suggest that head movements have no effect on the perception of surface slant. Another conclusion is that in the case of flat surfaces it is much easier to estimate slant, because the slant is the same at every position. Finally, these results indicate that the observers under the no-head-movement condition assume an amount of rotation, because a random movement led to random slant estimations. They interpret more movement as a larger slant and less movement as a smaller slant.

◆ **Response times to centripetal and centrifugal motion in the upper and lower visual field**

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Mateeff et al (1991 *Vision Research* **31** 131–138) found that with single moving targets subjects tend to respond faster to centripetal than to centrifugal stimuli. This anisotropy was obtained with simple reaction times, monocular observation, and horizontal motion. We studied whether a similar anisotropy holds for choice reaction times (RTs), binocular observation, and vertical motion. After a constant period, a small (diameter 12 min) light began to move at 2 deg s^{-1} upward or downward along the upper or lower vertical meridian, starting at 4, 8, 12, or 16 deg from fixation. Subjects responded with either their right index or their right middle finger according to whether the light moved up or down. (To balance out possible motor asymmetries, each stimulus direction was responded to by one finger in one session and by the other in another). Mean RTs were generally shorter in the lower visual field than in the upper (38.6 ms), as we found before (Ehrenstein et al, 1991 *Pflügers Archiv* **418** R39). Averaged over fields, centripetal RTs were 12 ms shorter than centrifugal. This difference was not significant, whereas the interaction (direction \times field) was: centripetal RTs were faster (39.7 ms; $p < 0.05$) in the upper field, but slower (15.8 ms; $p > 0.10$) in the lower. Thus responses tend to be faster to downward motion be it centripetal (upper field) or centrifugal (lower field), an anisotropy which tends to balance out the centripetal preference and is possibly related to the fact that objects commonly accelerate when falling and decelerate when moving upward in everyday life.

◆ **Speed discrimination of motion defined by binocular disparity**

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It has been proposed (Cavanagh and Mather, 1989 *Spatial Vision* **4** 103–129) that a common motion analysis underlies the processing both of first-order motion (luminance-defined) and of second-order motion (such as that defined by contrast, texture, or binocular disparity). This hypothesis is supported by the fact that speed discrimination is as precise for contrast-defined second-order motion as for first-order motion (Turano and Pantle, 1989 *Vision Research* **29** 207–221). Here, we show that speed discrimination for stereo-defined motion is very poor compared with that for luminance-defined motion. By means of a two-alternative forced-choice procedure, we measured speed discrimination for two types of stimuli. The first was a random-dot stereogram in which a rectangle stood out in depth with a disparity of 7 min (20–50 times detection threshold). The rectangle moved from left to right. This stimulus contained both stereo-defined and luminance-defined motion cues (the moving rectangular patch of dots was visible monocularly). The second stimulus was a dynamic random-dot stereogram in which the dots defining both the disparate rectangular region (with a disparity of 20–50 times detection threshold) and the background changed position randomly from frame to frame. Again the rectangle moved from left to right. This stimulus contained only stereo-defined motion (the rectangle and its motion could be seen only when the stimulus was viewed stereoscopically). For the first stimulus, Weber fractions ($\Delta v/v$) for speed discrimination were around 0.15 for a range of different speeds and dot densities. For the second stimulus (stereo-defined motion), speed discrimination was always poorer, with Weber fractions at least twice as large as for the luminance-defined motion. When we equated the two stimuli for apparent brightness and apparent dot

density, there was no improvement in performance for stereo-defined motion. These results suggest that stereo-defined motion does not support speed discrimination.

◆ **One or multiple motion systems?**

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Fourier (linear front-end filtering) motion models cannot extract directional information from stimuli which do not have energy along an oriented path in space-time. Humans can. A non-Fourier (nonlinear) motion system has been postulated to account for this. The possibility still remains that a unique, nonlinear transformation could account for both types of motion. The purpose in the present study was to test this hypothesis. Psychophysical experiments were run that involved two types of elements against a uniform background with luminance L_0 . The two types of elements were: 'L', with a uniform luminance $L \neq L_0$, and 'C', consisting of a random-dot texture with mean luminance L_0 , but nonzero contrast, C . The elements were arranged in space-time to produce two distinct stimulus configurations, each involving two competing motion paths, a homogeneous and a heterogeneous one. In configuration 1, the homogeneous path was L-L and the heterogeneous path was L-C. In configuration 2, the homogeneous path was C-C and the heterogeneous path was again L-C. The observer's task was to report the direction of motion in a two-alternative forced-choice paradigm. In both configurations C was fixed and L was varied to obtain a value (L_1 and L_2 , for configurations 1 and 2, respectively) for which motion was ambiguous. L_1 was the luminance which 'balanced' the paths L_1 - L_1 and L_1 - C ; thus, for a single motion system, L_1 produces a response which is equivalent to C . Similarly, L_2 balanced the paths C - C and L_2 - C , thus L_2 is also equivalent to C . Thus, under the single motion system assumption we expect $L_1 = L_2$. Our results indicate that this prediction is severely violated, offering evidence for the existence of multiple systems for the processing of motion.

◆ **Motion-contrast acuity and retinal eccentricity: a comparison of psychophysical and VEP measures**

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We investigated the effects of retinal eccentricity on motion contrast 'acuity' and VEPs. For this purpose, eight subjects were presented with a form-from-motion Landolt ring at retinal eccentricities of 0, 2, and 5 deg in the left visual hemifield. The observers had to indicate one of four possible positions of the gap in the ring. During stimulus presentation, VEPs were recorded at Oz, O1, and O2. Acuity (measured as percentage correct) was significantly poorer when stimuli were presented in the periphery. Analogously, the amplitudes of the prominent VEP components N2, P2, and N3 were significantly reduced. VEP latencies did not vary with stimulus eccentricity. N2, P2, and N3 amplitudes were highly and positively correlated with the acuity measure (correlations between 0.66 and 0.95). The slopes of the acuity and N2 amplitude functions were proportional to the magnitude of the 'cortical magnification factor', as quantified by Rovamo and Virsu (1979 *Experimental Brain Research* 37 495-510). The N2 amplitudes at Oz, in particular, were almost perfectly fitted by their equations. Thus, motion-contrast acuity appears to depend upon the magnitude of the 'cortical reference area' in V1. The implications of these findings are discussed.

◆ **Temporal sensitivity to changes in velocity of visual motion**

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Experiments are presented in which the ability of four observers to detect brief changes of velocity ('pulses') on the 'background' of another velocity was studied. A random-dot pattern moved at a baseline velocity V_1 within a stationary circular area (diameter 8.9 deg) located 4.5 deg above the fixation point. The velocity then increased or decreased abruptly to another value V_2 for a certain time and again returned to V_1 . The temporal threshold, ie, the duration of V_2 that was necessary for detection of the change, was measured. In experiment 1 the same velocity increment, $V_2 = 2V_1$, was presented, when V_1 was 1, 2, 4, or 8 deg s⁻¹. The threshold decreased significantly from 92.7 ms to 38.8 ms on average when V_1 increased from 1 to 8 deg s⁻¹. In experiment 2 a baseline velocity $V_1 = 2$ deg s⁻¹ was employed: V_2 was 4, 8, or 16 deg s⁻¹. Then these pulses were reversed; V_1 was 4, 8, and 16 deg s⁻¹ and V_2 was kept constant at 2 deg s⁻¹. The threshold decreased as the magnitude of the pulses increased, being

correspondingly 56.1, 19.0, and 8.1 ms for the three increments; the thresholds for the detection of decrements were significantly longer, 69.5, 40.0, and 31.3 ms, than those for the detection of increments. Two possible interpretations are considered. The first is based on the findings that higher velocities are detected by mechanisms that respond more rapidly, and integration of velocities occurs when temporally adjacent motions are presented (Nakayama, 1985 *Vision Research* **25** 625-660). The second is based on the hypothesis of Dzafarov et al (1993 *Perception & Psychophysics* **54** 733-750) that motion is detected when the running variance of the positions through which the stimulus passes during the motion exceeds a critical value. It is shown that the model of Dzafarov et al seems to be better in accounting for the data.

◆ **Spatial frames of reference in visual motion detection: independence or interference?**

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For a long time, vision researchers have studied visual motion by presenting it on a uniform, dark, or dimly illuminated background (Ganzfeld). At the same time, it has been recognised that both in natural and in laboratory settings, a moving object is usually surrounded by other objects which considerably affect the visibility of its motion (path, velocity, etc). Dynamic frames of reference (of a Johansson type) seem to be interrelated and hierarchically nested (Restle, 1979 *Psychological Review* **89** 1-24). Does this also hold for stationary spatial frames of reference in visual motion detection? We compared displacement thresholds for oscillatory motion of a thin bright line at temporal frequencies of 0.1-12.8 Hz in various spatial surroundings. The two main conditions were the presence and absence of a reference target near the moving object. In the latter case, motion was presented on dark backgrounds, moving-patterned backgrounds, and under dim illumination of the screen, when its peripheral borders were slightly visible. In the former condition, each of these backgrounds was combined with the reference target located just above the moving object, or at one of four positions up to 200 min laterally. Each experimental condition was tested in a separate series. The results indicate that, in general, the successive increase of separation between reference target and moving object, and then complete elimination of peripheral borders of the screen, gradually diminish motion sensitivity. In the presence of the reference, the threshold curves for dark, moving-patterned, and dimly illuminated backgrounds are the same. The absence of the reference yields a considerable decrease of the overall sensitivity for the conditions, although in the first two conditions above, the threshold curves coincide and the effects are significantly higher than for the third. The findings suggest that spatial frames of reference in visual motion detection are hierarchically organised, yet independent.

◆ **Flicker masking and apparent-motion perception**

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The effect of achromatic and equiluminant uniform flicker masking was studied in experiments on motion perception. The test stimuli were continuously presented vertical achromatic gratings within the range of 0.65 to 7.8 cycles deg^{-1} . In each trial the test was abruptly displaced to the right or to the left at differing phase angles (θ) and the threshold contrast for the detection of this displacement or for the discrimination of its direction was measured. The results confirmed the finding of Nakayama and Silverman (1980 *Journal of the Optical Society of America A* **2** 267-274) that the contrast sensitivity increased as $\sin(\theta/2)$ or $\sin\theta$, depending on the task (detection or discrimination, respectively). This notion was also extended for conditions of flicker masking. The masking effect was the highest (0.6 log units) at the lowest spatial frequency (0.65 cycle deg^{-1}), decreasing gradually to zero with the increase of the spatial frequency to 3.9 cycles deg^{-1} . In some experiments a static random noise was superimposed on the test gratings. This made the stimuli visible near the moment of displacement only and enhanced the role of transient signals in the task performance. In this case, the effect of the flicker was higher, decreasing gradually with the spatial-frequency increase to a higher crucial value (7.8 cycles deg^{-1}). Experiments with flicker of different amplitude demonstrated no saturation effect of the amplitude, typical of the dynamic properties of the magno pathway. The masking effect was also observed with equiluminant (red/green) uniform flicker and achromatic test gratings. These findings suggest that the uniform flicker deteriorates processing of transient signals initiated by low-spatial-frequency targets and that this deterioration might be realised by connections of the motion-specific mechanisms both with magno and with parvo pathways.

◆ **Visual-information-processing factors influencing the accuracy of complex movements without visual control**

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The role of visual-information-processing capacity (short-term memory span and simple and choice reaction time) in regulation of complex graphic movements was studied by means of the zigzags subtest of the Mira-y-Lopez myokinetic psychodiagnosis test (MKP). In testing, the subject has to draw zigzag lines with two hands at the same time, towards and away from his or her body in accordance with a model. The subject draws six zigzags with direct visual control, then a screen is placed in front of his/her eyes and the subject continues on the basis of the visuo-motor image formed earlier. Short-term memory span and reaction times to visual digit stimuli were analysed by means of a computer. We have previously demonstrated that the visual short-term memory span has a significant role in regulating the scatter of line and angle sizes drawn without visual control (Ryazanova et al, 1992 *Perception* 21 Supplement 2, 107-108). A new parameter for analysing the MKP results is discussed: the quantity of accurate reproductions of model size in the subject's performance (9.5-10.5 mm line length and 27°-33° angle size). The constancy of size on the basis of form constancy means increasing the adequacy of the formed image. The results show that (a) there are close links between all aspects of accurate reproductions of model size (including line-angle) with both hands and in both movement directions; (b) choice reaction time correlates with the quantity of accurate lines and angles—the shorter the choice reaction time the greater the quantity of accurate model reproductions ($p < 0.05$); (c) links with simple reaction times are not regular; and (d), unexpectedly, short-term memory span was not related significantly to accurate reproduction of model size. These results suggest that short-term memory span relates to regulation of 'relative' aspects of MKP performance (scatter), and speed of information processing relates to regulation of 'absolute' aspects (accurate reproduction of sizes).

◆ **Discrimination of direction of a constant-speed and accelerated or decelerated visual motion synchronised with EEG alpha-wave phases**

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Probability and latency of recognition of the direction (towards or away from the fixation point) and side (right or left hemifield) of randomly presented horizontal motion were studied in fourteen observers. Apparent motion was displayed on a computer-controlled row of thirty light diodes and its onset was synchronised or not synchronised (control) with different phases of occipital EEG alpha waves (Shevelev et al, 1991 *International Journal of Psychophysiology* 11 195-201). The speed of movement (6.3 deg path, 100 ms presentation) was either constant (63 deg s⁻¹) or accelerated/decelerated logarithmically during each trajectory to compensate for the cortical magnification factor for V1 (Covey and Rolls, 1974 *Experimental Brain Research* 21 447-454) and to produce an even spread of the evoked cortical excitation.

We have found (1) reliable increase in recognition probability for accelerated/decelerated versus constant-speed movement; (2) disappearance of the dependence of this probability on the alpha-wave phase in the case of constant-speed movement; and (3) pronounced (nearly 2 times) shortening of the response latency to the movement directed away from the centre of the visual field under synchronisation with alpha wave.

The data are discussed in relation to the hypothesis (Pitts and McCulloch, 1947 *Bulletin of Mathematical Biophysics* 9 127-147) on the EEG alpha wave as a scanning process that rhythmically spreads over the visual cortex for readout of information and timing of perception. Our data show that this spread is linear in cortical space and predicts the probable direction of the process.

◆ **Analysis of perceived motions of dynamic point configurations: mobile reference frames and minimum principles**

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Dynamic point configurations are stimuli consisting of a few points moving on a homogeneous background. As shown by Johansson [1950 *Configurations in Event Perception* (Stockholm: Almqvist & Wiksell)] and many others, such stimuli often involve a remarkable discrepancy between motions of points with respect to the background and motions of points as seen by observers. Most researchers agree that the notion of mobile reference frames is the key for the explanation of these phenomena. The problem is that there is an infinity of possible mobile reference frames for any configuration. Attempts to formulate a perceptually relevant law

of reference-frame motion have mainly had limited specificity or generality. In the present approach, such a law is derived through methods of the calculus of variations, standardly used in physics to derive laws from minimum principles. Three versions of a principle of least motion are formulated, involving a distance-based, a speed-based, and a path-based scalar global measure of motion of a dynamic point configuration. The derived law of reference motion can be applied to any type of point motion, and has the form of a weighted average of the absolute motions of the points and a constant vector. The weights reflect the extent of minimisation of reference-frame motion and minimisation of relative motions of the points. Diagrams of predicted reference-frame motions and relative motions provide convenient visualisations of the law. The theory can account for most published data on dynamic point configurations. Furthermore, it correctly excludes the possibility of some plausible percepts that are in fact not empirically realised. The choice of the size of the weights in the majority of cases is governed by the viewing instructions (free scanning, tracking one of the points, or stationary fixation). However, in some cases the reference-frame motion is independent of eye motions and is determined by the structure of the stimulus.

◆ **Apparent-motion perception in the left and right peripheral visual field**

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Recently Osaka (1993 *Perception* 22 Supplement, 80–81) has shown the superiority of the lower visual field for seeing apparent motion. One can consider this difference as some kind of 'functional anisotropy' of the visual field. We investigated whether such anisotropy existed for the left and right visual hemifield. A subject fixated the centre of a computer display where a digit was presented in a random order for 500 ms. At the end of this interval a target was presented in a random order in the left or right visual hemifield at 10 deg eccentricity. The target was a small white ring (diameter 6 pixels, or about 20 min) which moved in the horizontal or vertical direction (speed 20 deg s⁻¹, duration 250 ms). The subject's task was to detect the target and determine its direction. Each session consisted of 600–800 experimental trials. The contrast of the target was reduced to make this task more difficult for a human observer. Five subjects (right-handed, with normal vision) participated in the experiment. Four demonstrated a superiority of the left visual hemifield ($p < 0.05$); one had a similar tendency but the difference was not significant. In addition a majority of subjects demonstrated a superiority for detection of targets which moved upwards (versus downwards). The superiority found of the left visual hemifield in apparent-motion perception may reflect the superiority of the right hemisphere in visual perception.

◆ **Visual discrimination of complex moving configurations: an inverted biological-motion pattern in usual and reverse transformation**

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In the study of biological-motion perception, discrimination of lateral movement of a 'hidden' object (represented only by a set of moving dots) serves as an indicator of its structure extraction. Yet, observers may use another (more simple) stimulus parameter which is related to seen lateral object movement, but not necessarily to structure extraction (eg relative motion of its elements). We examined this possibility by using an upside-down (180°) biological-motion pattern presented in usual (A) and reverse (B) (produced by showing the film frames in the opposite direction) transformations. The display consisted of an array of moving bright dots located on the main joints of an invisible animal facing right and moving as if on a treadmill. As previously shown (eg Pavlova, 1989 *Perception* 18 510), such an inversion of a biological-motion pattern completely prevents recognition of its structure. An experimental session contained demonstrations of A and B examples and then an equal number of randomly distributed test trials of both types (total of sixty-four trials of 3 s duration each). In each trial, the film fragment presented was randomly selected from the whole succession of frames. Subjects accomplished a binary classification of the stimuli (is it an A or B display?). The results indicated that observers are able to discriminate the displays reliably. Since both moving configurations possessed the same structure, these were discriminated only on the basis of relative-motion direction of their elements. It is suggested from the data that one should use perceived lateral movement carefully as an indicator of observers' extraction of implicit object structure in biological-motion patterns (cf Cutting et al, 1988 *Perception & Psychophysics* 44 339–347). Besides, the finding reflects a general tendency of an observer to use spontaneously the most salient stimulus parameter while accomplishing a discrimination task.

◆ **Does perceived speed of translating plaids depend only on second-order motion signals?**

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When two identical gratings are drifting with the same speed in different directions, they are perceived as a rigidly translating two-dimensional pattern (a plaid). How does the visual system integrate these two components in order to estimate a global speed? A plaid appears to move more slowly than predicted by the intersection-of-constraints (IOC) model when its speed is judged against a reference stimulus (a grating) whose spatial frequency is the same as that of the components (Ferrera and Wilson, 1991 *Vision Research* 31 877–893). A crucial point is that this underestimation increases with the angle (α) between the directions of the components. According to Ferrera and Wilson, apparent speed is not based on the first-order motion of the components but rather on the second-order-motion signal (SOMS) available in the plaid—this signal corresponds to the distortion product, which has the same velocity as the IOC resultant. Indeed, when α is increased, the spatial frequency of the SOMS becomes lower, which could be the reason why apparent speed decreases (although the effect of spatial frequency on apparent speed is still controversial in the literature). As suggested elsewhere, however, (Castet et al 1993 *Vision Research* 33 1921–1936) this decrease of apparent speed might be due to the lower speed of the components (relative to the IOC speed) accompanying larger angles α .

In order to distinguish between these two propositions, in the present study we measured the perceived speed of plaids having a constant IOC speed and a constant second-order spatial frequency but different speeds of the components (and thus different angles α). This latter constancy was achieved by increasing the spatial frequency of the components when α was increased. The speed of the reference stimulus (a line moving in the direction of the plaid) was adjusted by means of two staircases converging on 29% and 71% thresholds. The point of subjective equality for each plaid was assessed by taking the mean of these two thresholds. Calculation of the differential threshold (half the difference between the two thresholds) allowed estimation of the precision with which speed was encoded. The main finding is that, for most observers, apparent speed of the plaids decreases with the speed of the components. This shows that SOMSs cannot be the unique basis for speed encoding of a plaid since the components (first-order signals) are able to bias the global perceived speed.

◆ **Implications of the multichannel gradient model of motion processing for an understanding of the response properties of cortical cells**

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Although the computation of motion from spatiotemporal gradients of image brightness is often used in computer vision applications, this approach to motion computation has been considered less attractive for modelling motion processing in the human visual system than alternative models which appear to allow a more straightforward biological implementation. One aim for the multichannel gradient model (Johnston et al, 1992 *Proceedings of the Royal Society of London, Series B* 250 297–306) is to provide a rapprochement between the motion-from-spatiotemporal-gradients computational strategy and the evidence of multiple spatiotemporal channels in the human visual system. The model incorporates a number of clearly identifiable processing elements and stages. Here we examine in some detail how the components of the model may be mapped onto the classes of cells found in mammalian primary visual cortex. The image is convolved with a range of blurred differentiating filters. Since higher-order differentiating filters are tuned to higher spatial frequencies this gives rise to a range of spatially tuned 'channels'. Some of the filters compute a temporal derivative. This gives two classes of filters which may be described as sustained or transient on the basis of their temporal response properties. We find we require two transient channels in order to model the effects of the introduction of a blank interframe interval in a sampled motion sequence. Products formed between the sustained and transient filters provide a directionally selective output which is independent of polarity of contrast. The outputs of the sustained filters are squared, giving a full wave-rectified response. Note that the rectification is required to condition the quotient in the gradient model—it is not a separate preprocessing stage as in other motion models. The output of the model provides a phase-independent response to drifting sinusoidal gratings similar to that found in complex cells.

ELECTROPHYSIOLOGY AND CLINICAL RESEARCH

◆ Corpus callosum section modifies the functional characteristics of neural receptive fields of cat prestriate cortex

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The experiments were performed on eighteen immobilised cats weighing 2.5–4 kg. During the operation, 2–4 days before the experiment, the skull was opened to expose cortical area 21 and total corpus callosum section was performed. Data obtained before and after section of the corpus callosum are presented. In the study of the properties of single neural receptive fields (RFs) in the prestriate cortex, interhemisphere differences are revealed. The neural RF sizes in the left hemisphere of the intact animals were almost 1.5 times larger (25–60 deg) than in the right (10–40 deg). 68% of neurons in the left hemisphere were unaffected by stimulus orientation; in contrast, many neurons in the right hemisphere were selective to stimulus orientation. 66% of neurons in the right hemisphere was characterised by directional selectivity, while in the left only 33% of them showed this characteristic. In the neural RFs of the left hemisphere a larger part (up to 40%) of the ipsilateral hemifield of vision was represented than in the right hemisphere (up to 20%). The result of the commissurotomy was the disappearance of interhemisphere differences. The sizes of RFs were significantly less and became equal in both hemispheres (average 26 deg). The principal result of section of the corpus callosum is complete loss of the ability to describe invariant images: the neurons of this area become selective to stimulus orientation and direction of stimulus movement in both the left and the right hemisphere. In this case the hemisphere fully lost the ability to receive information from the contralateral hemisphere, that is, the hemispheres lost representation of the ipsilateral hemifield of vision. It should be noted that after corpus callosum section one may observe an asymmetry of head orientation (tilt and roll) which was compensated after 2–4 days. On the basis of clinical and psychophysical studies it is generally accepted that the two aspects of visual perception—concrete and abstract—are to a certain extent separate and realised mainly by different hemispheres. It is suggested from the results of this study that the intact brain is able to describe and identify the images as a whole only when the two hemispheres interact.

◆ Inhibitory zones in the receptive fields of visual neurons determined by moving stimuli

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Receptive fields of forty-one visual neurons from the Clare-Bishop area of the cat cerebral cortex were investigated in order to examine the spatial arrangement of inhibitory zones. The spatial structure of receptive fields (RFs) was constructed from the PSTH obtained from responses to a moving light spot. All RFs investigated can be divided into two groups: (1) those composed only of active zones (eleven neurons); (2) those composed of active and inhibitory zones (twenty-five neurons). Five neurons had a very low level of spontaneous activity; therefore it was difficult to estimate inhibitory activity. The spatial structure of RFs in the second group of neurons is more complicated—the inhibitory zone does not lie within the active zone, but can be distributed in three different ways: (1) a bigger or smaller half-ring-shaped area on one side of the active zone (twenty-one neurons); (2) two separated half-rings on two opposite sides of the active zone (seven neurons); (3) surrounding the active zones as a single ring (one neuron). It was found that area of the inhibitory zone is bigger when the stimulus moves towards the centre from the outside if compared with the case when the stimulus moves from the centre to outside the RF.

◆ The role of inhibition for orientation tuning and its dynamics in the cat striate cortex

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Many neurons in the cat visual cortex reveal a successive shift of their preferred orientation with time during response generation (Shevelev et al, 1993 *Neuroscience* 56 865). We investigated this effect before and after the blocking of GABAergic inhibition by microiontophoretic application of bicuculline. Typically, orientation tuning changed profoundly after bicuculline application in the great majority of cells under study (forty-three). The response magnitude increased fivefold on average, the mean background frequency fourfold, orientation tuning widened to 32.0° ($p > 0.01$), while tuning selectivity decreased sixfold.

Dynamic estimation of orientation tuning before and after bicuculline application revealed two main types of change. Neurons with a relatively large dynamic shift of the preferred orientation typically diminished ($-69.9^\circ \pm 10.1^\circ$) or lost this shift after blocking of GABAergic

inhibition (nearly one third of units), while neurons with a smaller shift of preferred orientation or without a shift (more than half of the units) revealed an increase ($+79.0^\circ \pm 7.0^\circ$) or appearance of the dynamics after bicuculline application. The results indicate considerable involvement of intracortical inhibition in orientation detection, as well as the different contributions of this inhibition to the different response types of visual cortical neurons distinguished by the stability or time dependence of their orientation preference during response generation. The possible functional role of the two groups of neurons in orientation processing in relation to its temporal aspects is discussed.

◆ **Apparent latency of pattern-reversal and on-off VEPs**

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The steady-state VEP response to pattern-reversal stimulation has characteristics which seem to conflict with psychophysically obtained response properties. Both amplitude and temporal phase are highly variable between subjects and, moreover, amplitude often shows a notch, being paradoxically attenuated at medium spatial frequencies. On-off modulation at high rates (around 16 Hz) is very similar across subjects with amplitude similar to the contrast-sensitivity function and phase largely independent of spatial frequency. Using factor analysis, we have previously shown that pattern reversal elicits more-complex responses than does on-off. In the present study we investigated differences in temporal-phase response between these kinds of modulation, using Diamond's (1977 *Electroencephal. Clin. Neurophysiology* **42** 125-127) 'derived'-latency and Regan's (1972 *Evoked Potentials* (Andover, Hants: Chapman and Hall) 'apparent'-latency technique. The two spatial frequencies were chosen to be either side of the medium-spatial-frequency notch. Temporal phase to on-off stimulation shows a linear relationship with modulation rate over a 1-octave range of rates (10 Hz to 20 Hz). Its slope is largely independent of spatial frequency. Pattern-reversal stimulation leads to a nonlinear relationship of temporal phase with modulation rate; at least two regions of different phase-vs-frequency slopes can be distinguished. These slopes also depend on spatial frequency. The derivation of latency is thus straightforward for on-off modulation. Furthermore, the notion of a simple, pure-delay system underlying the on-off response is supported. The more-complex phase/temporal-frequency function from pattern reversal can be interpreted either as two systems interacting or as the presence of an additional filter stage in the pathway.

◆ **Temporal tuning of direction selectivity in visual cortex neurons: a reverse correlation analysis**

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In previous studies it has been shown that single neurons in mammalian visual cortex show direction selectivity to two-flash apparent-motion stimuli. Typically there is an optimal spatial displacement which is slightly less than one quarter of the period of the optimal spatial frequency of the neuron (quadrature phase), in good agreement with similar findings from human psychophysics (Baker et al, 1991 *Vision Research* **31** 1659). However, the temporal properties of such two-flash direction selectivity have proven difficult to measure, owing to the substantial integration times of most cortical neurons.

Here a 'reverse-correlation' analysis was used, in which the averaged responses of a single neuron to random ternary stimuli (Emerson et al, 1987 *Journal of Neurophysiology* **58** 33) were used to measure the optimal spatial and temporal separations for interactions underlying direction selectivity. Typical results were as follows: (1) bandpass tuning to temporal separation, (2) differing optimal values of temporal separation in different neurons, (3) optimal temporal separations in an approximate quadrature-phase relationship, and (4) a range of optimal temporal separations roughly comparable to the range of effective values found in human psychophysics, though shifted to somewhat smaller values (possibly owing to the higher luminances used here). The spatiotemporal properties measured with this technique are consistent with those of the 'quasi-linear' (but not the 'nonlinear') mechanism described by Boulton and Baker (1993 *Vision Research* **33** 1803; 1993 *Vision Research* **33** 2013). These results are consistent with the idea that the bandpass dependence of human motion perception on temporal (as well as spatial) intervals (Morgan and Ward, 1980 *Vision Research* **20** 431; Baker et al, 1991 *Journal of Neuroscience* **11** 454) represents an envelope of more-narrowly tuned direction-selective mechanisms.

◆ **Changes of contrast sensitivity in patients with endocrine ophthalmopathy**

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In endocrine ophthalmopathy compression of the optic nerve is one of the main lesions. In early stages of this disease routine ophthalmological tests do not reveal any functional changes in the eyes. We measured contrast sensitivity in thirty eyes of sixteen patients with endocrine ophthalmopathy. Their age was 24–61 years (mean 44.9 years), their mean proptosis was 16.25 ± 2.5 mm, and their corrected visual acuity was normal. Contrast sensitivity was measured by means of Volkov's charts (sinusoidal gratings) at eight spatial frequencies from 17.5 to 0.46 cycles deg^{-1} . The age-matched control group consisted of twelve healthy persons with normal visual acuity. Contrast-sensitivity threshold was increased by about 15% at high spatial frequencies ($p < 0.0001$), by about 5% at spatial frequencies of 6.5 and 3.4 cycles deg^{-1} ($p < 0.0007$), by 3% at a spatial frequency of 1.7 cycles deg^{-1} ($p < 0.0125$), and at low spatial frequencies by 5% ($p < 0.0001$). It is suggested from the data that contrast-sensitivity testing allows earlier detection of functional changes in the eyes in endocrine ophthalmopathy.

◆ **Oscillating stimuli as a tool to investigate MT and MST cells of the awake monkey**

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In most electrophysiological experiments on visual responsive cells in areas MT and MST, stimuli are used which move at constant velocity. For stimulation in area MT a drifting grating is often used. For area MST one usually presents optic-flow patterns (divergence, convergence, rotation, etc) in single trials, interrupted by pauses to sample background activity. In the current study, similar optic-flow patterns were used, but they were presented as oscillating stimuli in an attempt to gain more insight into the dynamics of the responses of these cells. In the present experiments on awake monkeys, cells in areas MT and MST were tested with oscillating patterns of random dots with finite lifetimes. Frequencies ranged from 0.25 to 4 Hz. In addition, perturbations were introduced to study the relaxation times after 180° phase shifts. All cells investigated responded very well to the oscillatory movements, provided the effective optic-flow component was present. Responses decreased and phase locking was poor for frequencies above 2 Hz. After perturbation, relaxation times were in the order of 250 ms, indicating a tight coupling between response and stimulation. One cell gave only a very small response to nonoscillating optic-flow stimuli, but responded vigorously to periodic stimulation in the preferred direction. The latter result, and more generally the greater efficacy of oscillating stimuli, are thought to be due to summation of disinhibition, following stimulation in the nonoptimal stimulus direction, and facilitation due to movement in the preferred direction.

◆ **Dynamic dissection: extracting information from noisy spike trains in the central nervous system**

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We compared intracellularly recorded ganglion-cell responses in the cat retina with computer simulations of a retinal network model. The model includes the membrane properties of ganglion cells. Intracellularly recorded responses of retinal ganglion cells to sinusoidally flickering light spots were separated into the 'slow' generator potential and the concomitant spikes. Detailed analysis of the generator potential reveals at least two components. One component is directly correlated and phase locked to the stimulus, while a second, faster, component shows no phase lock. The experimental generator-potential responses could be described by the externally forced van der Pol equation (Przybylski et al, 1993 *Vision Research* 33 861). The transformation of the generator potential into spike trains involves complex membrane properties, as described by the extended Hodgkin-Huxley equations (which are based on patch-clamp data). Thus, the information in the ganglion-cell spike trains comprises, in addition to the components in the generator potential, a third component that is related to the membrane properties of the ganglion cell that are involved in spike generation. Ganglion-cell spike trains therefore reflect the interaction of multiple dynamic components. Irregularities in the spike train can be interpreted as the result of complex oscillations rather than as irrelevant noise. The simulated model, which incorporates an externally forced van der Pol equation as well as the Hodgkin-Huxley equations, enables us to dissect the experimentally observed responses of cat retinal ganglion cells into their different components. This analysis separates stimulus-related

responses from the response characteristics determined by network interactions and membrane properties. We show the value of this analysis for ganglion-cell responses and propose its application to other parts of the central nervous system. The 'dynamic dissection' is much more informative than classical methods based on spike-train averaging, especially if the generator potential of the neuron can be recorded.

◆ **Spatiotemporal motion-response characteristics of complex cells in cat area 17**

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The use of moving random-dot patterns in human psychophysical experiments has contributed enormously to our understanding of the mechanisms involved in motion perception. Relatively little information is available, however, on the responses of motion-sensitive cells in the visual system to these stimuli. We have studied the characteristics of directionally selective cells in area 17 of the cat by means of moving random-pixel arrays (RPAs), similar to those used in human psychophysics (see Fredericksen et al, 1993 *Vision Research* 33 1193-1205). The apparent-motion stimulus consists of moving RPAs (50% dot density) with pixel lifetimes limited to two frames and therefore contains motion energy for only a single spatial-displacement/temporal-delay combination. We recorded the responses of complex cells to different combinations of displacement and delay to describe their spatiotemporal correlation characteristics. The mean luminance of the RPA was 50 cd m⁻² and the contrast was 70%. At the viewing distance of 57 cm the pixels subtended 3.2 min × 3.2 min. Adult cats were anaesthetised with a 70:30 mixture of N₂O:O₂ supplemented with 0.1%-0.4% halothane. The eyes were immobilised by administering galamine triethiodide intravenously (10 mg kg⁻¹ hr⁻¹). Our sample of cells consists of complex cells responding very vigorously to moving RPAs. The responses were direction selective, and optimal at one spatial displacement and temporal delay. A stimulus containing this preferred displacement still causes some direction-selective response at delays longer than the preferred delay of the cell. The preferred displacement is equal to the maximum displacement that gives a directional response when moving RPAs with unlimited pixel lifetimes are used. These results show that low-level directionally selective cells are tuned to a single combination of displacement and delay. This finding is in agreement with previous human psychophysical results.

◆ **Threshold of visual sensitivity in patients with thyroid optic neuropathy**

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Optic nerve dysfunction is a most worrisome complication of endocrine ophthalmopathy. It is not related to the degree of exophthalmos but depends more on the degree of extraocular muscle swelling in the apex of the orbit. The problem of threshold sensitivity in patients with thyroid optic neuropathy has not been much investigated. The purpose of the present study was to investigate the threshold of visual sensitivity in patients with thyroid optic neuropathy. Twelve patients (twenty-four eyes) with thyroid optic neuropathy were examined. Eight patients were female, four male. Their ages ranged from 53 to 67 years. The control group consisted of fifteen healthy persons of similar age.

Visual acuity was reduced in fourteen eyes. Protopsis was from 17.5 mm to 23.5 mm. Both eyes were tested in randomised order with threshold-measuring automated perimetry, by means of the programs for the central 30 deg, and peripheral 30-60 deg. The mean sensitivity of the central visual field was significantly lower in comparison with data from the control group (26.1 ± 1.5 dB, $p < 0.001$). The reduction of mean sensitivity of the peripheral field also was noted (16.3 ± 1.3 dB, $p < 0.001$). It was established that a reduction of light sensitivity accompanies the decrease of visual acuity in patients with thyroid optic neuropathy. These quantitative characteristics of visual sensitivity provide us with valuable objective and additional information on the diagnosis and prognosis of patients with thyroid optic neuropathy.

◆ **Characteristics of tuning to cross-like figures in neurons of the cat striate cortex**

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Previously we described qualitatively the selectivity to cross-like figures in nearly one-third of neurons in the cat striate cortex (Shevelev et al, 1993 *Perception* 22 Supplement, 138). That means that such cells showed reliably better response to a restricted range of orientation and configuration of cross-like figures in comparison with their response to the preferred orientation of a single light bar. Detailed study revealed that twenty out of fifty-nine units increased their

response magnitude on average by a factor of 3.96 ± 0.6 (limits 2.4–12.9) under stimulation of their receptive fields by the cross-like figure of optimal orientation and configuration, in comparison with their response to the preferred orientation of the single light bar. In twelve of these neurons the selective index (ratio of responses to preferred and nonpreferred stimuli) increased by a factor of 9 (limits 1.7–34), while general tuning quality (directly proportional to selectivity and inversely proportional to tuning width) increased in fourteen units by a factor of 8 times (limits 1.9–43). Tuning width for the cross-like figures decreased (tuning sharpened) in comparison with orientation tuning to the single bar in nine neurons ($M \pm m = -66.7 \pm 14.3^\circ$). Thus, quantitative analysis confirmed our supposition that most of the cat striate neurons with selective sensitivity to cross-like figures are real candidates for angle and/or line-cross detectors. Possible mechanisms for the effect described and the functional meaning of such cells in cortical visual processing are discussed.

◆ **Visual agnosias: testing, rehabilitation, and theoretical substantiation by a neural network with damaged neurons**

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It is emphasised that perception involves making structural descriptions from the data and testing inferences as to what these data 'mean' for an object. Features that are especially useful in the analysis are brightness, contours, corners, edges, vertices, nearness, and so on, and there is evidence for cortical detectors for all of these features. Subjects with visual agnosias can see only one object (or feature of the object) at a time, rather than a whole field or whole image.

Four patients with visual agnosias and hemianopsias, four patients with hemianopsia, and four control patients were tested to determine the various sorts of visual agnosias. Visual acuity of all these persons was normal. A set of computerised tests, from primitive images to the most complicated ones, was constructed. An interactive approach for extracting main surface and spatial details from the tests was used. An artificial neural network with damaged neurons was simulated to imitate the activity of specified parts of the brain. A faster training algorithm was sought. Experiments were conducted and we came to the conclusions that by means of these tests we could determine visual agnosias and their complexity; that these tests could be applied for training persons with visual-perception disorders; that visual hemianopsias had no influence on visual agnosias; and that training with an artificial neural network with damaged neurons, training speed, and error analysis allowed us to form a new view of the complexity of cognitive processes.

◆ **Size discrimination in humans with hemineglect of the visual field and visual agnosia**

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Posner et al (1987 *Neuropsychologia* 25 135) demonstrated that patients with unilateral spatial neglect had a specific inability to disengage their attention from a given object in order to reallocate it to another object positioned to its left.

In the present studies we determined whether size-discrimination abnormalities in the neglected side also occur. We estimated the accuracy with which subjects judged the height of a circle and a square as being equal. Four groups of subjects participated in the experiments: (i) eleven persons with right-visual-field hemineglect, (ii) eleven with left hemineglect, (iii) eight with partial visual agnosia, and (iv) fifteen with undisturbed vision. Outline circles and squares with sizes from 0.2 to 3.0 deg were generated on a monitor. Circles were present on the left half, and squares on the right half of the screen simultaneously. Subjects viewed the patterns binocularly at a distance of 1 m and adjusted the size of the square to make its height equal to that of the circle. The error value of perceived linear dimensions were measured as a function of stimulus size. It has been reported (Loginovich et al, 1993 *Perception* 22 Supplement, 120) that perceived equality of the two figures is different from physical match, a square being about 5–10% bigger than a circle. In our experiments, only one subject in group (i) demonstrated a pattern of size illusion of relatively stable strength. Ten of the eleven failed. In group (ii) the results for seven subjects resembled the normal size-illusion data. In group (iii), seven of the eight showed irregular errors. All controls [group (iv)] showed the normal pattern. The data obtained provide evidence that humans with left-hemisphere injury show a deficiency, while those with right-hemisphere injury show better skills in size-discrimination procedures.

◆ **Physiological and clinical aspects of the rehabilitation of vision in optic-nerve atrophy**

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Data from the application of indirect periorbital electrical stimulation of damaged optic nerves have been analysed. Results are presented concerning the changes in physiological indices

during therapeutic electrical stimulation which provide evidence of the activation of peripheral and central links in the visual system of the brain under the influence of this stimulation. The visual effects of the novel technique, obtained from 1684 patients with optic-nerve atrophy of hypertensive, infectious, posttraumatic, toxic, vascular, congenital, and postglaucomatous origin, are summarised. The dependence of the probability of visual rehabilitation on the initial degree of visual disorder, and the physiological mechanisms underlying the improvement of visual perception are discussed. The efficiency of the novel technique treatment of optic-nerve atrophy and its advantages (due to its safety) over the previously developed methods of direct electrical stimulation of the optic nerve are demonstrated.

◆ **Some neuronal mechanisms of analysis of global visual features in the guinea pig striate cortex**

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In experiments carried out on the guinea pig striate cortex the following neuron properties were revealed which may be related to neuronal mechanisms of analysis of global visual features. (i) Atypical influences—about one third of the neurons tested ($n = 61$) had a poor excitatory response to a visual stimulus presented beyond the classical receptive field. Such atypical influences may constitute a low-level basis for analysis of contextual and global visual features. (ii) Double orientation tuning—about 40% of the striate cortex neurons tested ($n = 360$) were tuned to two orthogonal orientations. Most of these neurons had oscillatory activity (up to 6 phases with frequency about 40 Hz) in response to long optimally oriented bars and were located mainly in layer 5. Such neurons may identify the nodes of linking of local oriented image elements. (iii) 'Firing' of intracortical connections—short-latency excitatory connections were identified by cross-correlation analysis for 6 neuron pairs ($n = 128$) in response to long optimally oriented bars. In all cases the source neurons of the excitation were recorded in layer 4, while the target neurons were located in layers 3 or 5. Such intracortical connections being effective under long stimuli only may be a possible mechanism for the known stimulus-dependent synchronisation of striate cortex neuron activity. The contribution of these properties of striate cortex neurons to the analysis of global visual features was analysed by mathematical modelling.

◆ **Principles of visual recognition by brain neurons of the frog**

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Experiments were performed on frogs immobilised by tubocurarine and anaesthetised by novocaine. Neuronal activity was recorded from retinal ganglion cells and from neurons of the tectum, tegmentum, thalamus, and hippocampus. The following types of visual stimuli were used: diffuse illumination, stationary and moving spots, and oriented bars moving in different directions with different velocities. It was shown that the detecting neurons and the neurons which permit analogue description of signal features are represented in all structures of the frog's visual brain. However, their distributions were different at the different levels of the visual brain. Detecting (narrow-band) neurons are predominant in the retina, narrow-band and wide-band neurons have an equal distribution in the midbrain, wide-band neurons are predominant in the thalamus, and representation is random in the hippocampus. Thus the recognition of visual stimuli parameters is accomplished by means of two mechanisms—by narrow-band neurons that compute some discrete parameters of the visual signals, and by wide-band neurons that allow their continuous description. These two mechanisms added to each other may be adequate for full description of the visual image and the organisation of the motor reaction.

◆ **Properties of burst activity of visual cortex neurons and a strategy for detection of their responses to a light stimulus**

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Spontaneous firing and responses of nineteen individual neurons in the visual cortex of anaesthetised, paralysed cats were analysed quantitatively. The peristimulus time and spontaneous-activity histograms were transformed so that the average number of spikes of spontaneous activity was assumed to be equal to zero. Excitatory and inhibitory bursts (group discharges) were detected, then the number and the frequency of spikes in each burst were calculated. Correlation between the number and frequency of spikes and the average level of spontaneous activity was positive. The parameters of spike bursts fluctuated over time in a narrower range than the average frequency of spontaneous activity. The fluctuation of number of spikes, frequency

of bursts, and average number of spikes occurred in sequential 400 ms segments of the spontaneous-activity histogram. In order to assess a threshold for response, the number and frequency of spikes in the bursts before and after the stimulus were compared. To exclude fluctuations in the number and frequency of bursts, during the bursts the threshold for another histogram for the same neuron was used if the average frequency of spontaneous activity was within a range of 80 spikes per second around the average level of the histogram being analysed.

◆ **Contrast-sensitivity changes after transcutaneous electrostimulation of visual pathways**

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Contrast-sensitivity (CS) functions were investigated in thirty-six young (aged 12–20 years) subjects with myopic refraction disorders whose visual acuities were from 1.5/20 to 10/20, and in thirty-six control subjects whose visual acuity was normal. Testing was performed in three phases. (1) CS testing was undertaken at six spatial frequencies (0.4 – 18 cycles deg^{-1}) with an electronic video device at central fixation. CS functions were measured in photopic illumination. The subjects with normal visual acuity whose CS functions were normal at all frequencies were compared with refraction-disordered subjects whose CS functions were more or less reduced at all spatial frequencies, but especially at low and high frequencies. The lower the visual acuity and the greater the refraction disorder, the lower the CS function for all, but especially for high, frequencies. The results of testing validate the earlier findings that all frequencies of CS are at a low level in low-vision subjects. (2) An electrostimulator, ESO-2, was used to activate the visual system by transcutaneous stimulation in different conditions. During electrical stimulation the optic nerve was excited, and the excitation was controlled by the parameters of elementary visual sensations—the phosphenes. The thresholds of phosphene initiation were selected individually. The amplitude of current was 50 – 200 μA . (3) The first phase of testing was repeated after ten procedures of transcutaneous electrostimulation of the visual pathways. An improvement of contrast sensitivity and visual acuity was achieved in 85% of cases. The results suggest that transcutaneous electrostimulation is a new method for improving visual functions and contrast sensitivity.

◆ **Role of the vestibular analyser in space perception**

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The purpose in the present study was to elucidate the mechanisms leading to the false perception of motion and the shape of coloured targets as a result of vestibular analyser excitation. The study involved one hundred patients with disturbances at different levels of brain structure.

A method developed under clinical conditions was used. Coloured 45 W lamps with 35 cm between them were assembled in the following sequence on a metal panel: red, yellow, green, blue, violet. White lamps were installed at each end of the panel. The panel was in a horizontal position at a height of 2 m and at a distance of 2 m from a swivel chair. Vestibular stimulation was carried out by rotation of the chair. At the moment that the swivel chair stopped the patient was asked to indicate the direction of motion and the shape of the lamps.

Experimental results show that the speed of the false motion of the lamp (in the direction of the fast component of the nystagmus) depends on the colour. The greatest speed appears for the white lamps. The speed depends also on the brightness of the source position and on its remoteness. All patients reported an apparent change of the shape of the coloured targets—the elongation coincides with the slow phase of the nystagmus. In 72% of the patients there was a deviation in the perception of coloured targets; in 5%, motion of the red lamp; in 8%, motion of other coloured targets; in 7%, motion delay; in 15%, fast motion of colored lamps. In patients with labyrinthitis the tendency predominates of false fast motion of coloured targets or of its combination with other colours. In patients with brain disturbances the inverse tendency is present.

◆ **Object recognition in low-vision children with congenital brain or eye disease**

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In this study we compare object-recognition performance in children with congenital low vision due either to eye disease ($N = 70$) or to brain damage and eye disease ($N = 30$). In both groups age ranged from 5 to 21 years, verbal IQ ranged from 44 to 110, and grating acuity ranged from 2 to 16 cycles deg^{-1} . Object-recognition performance was measured in three ways:

naming of normal line drawings, naming line drawings masked by random noise, and matching overlapping line drawings. Each target drawing was presented on a computer screen for 1 s in the naming tasks and for 6 s in the matching task. First, performance in the low-vision group as a whole was compared with the performance of a group of normal children ($N = 101$) matched for age and mental level and with visual acuity higher than $16 \text{ cycles deg}^{-1}$. Performance was better in the normal than in the low-vision group for all three tasks. In both groups performance did not vary with age and mental level. Although performance in the low-vision group covaried with visual acuity, the interindividual variability was considerable. For instance, some subjects in the lowest-visual-acuity group ($2\text{--}4 \text{ cycles deg}^{-1}$) performed better than some in the highest-acuity group ($10\text{--}16 \text{ cycles deg}^{-1}$). Second, the low-vision group was subdivided according to aetiology. Although both subgroups showed an equal distribution of visual acuity, it was found that recognition performance was more impaired in the brain-damage group as compared with the eye-disease group. These findings suggest that there is more to low vision than vision impairment.

◆ **Velocity tuning of cat parabigeminal neurons**

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Visual responses of single neurons of the cat parabigeminal nucleus, a satellite system of the superior colliculus, were registered. In cats with pretrigeminal brainstem transection, single-unit activity was recorded extracellularly in eighty-four neurons. Moving or stationary black or white stimuli of different sizes and shapes were projected by means of a slide projector. All neurons but one responded to the moving stimuli. Forty-one cells were tested in detail with stimuli varying in speed from 5 to 360 deg s^{-1} . Most of the cells showed broad velocity tuning, with the strongest responses evoked by stimuli moving at velocities of $35\text{--}70 \text{ deg s}^{-1}$. The mean preferred velocity was $61 \pm 9 \text{ deg s}^{-1}$. Six neurons preferred slower velocities ($10\text{--}20 \text{ deg s}^{-1}$) and five neurons preferred velocities equal to or higher than 140 deg s^{-1} . The highest preferred velocity that we observed was 360 deg s^{-1} (one neuron). The velocity-tuning curves and optimal velocities for a given cell varied with the different shapes and contrasts of the stimuli; they were also different when the cell was activated through the ipsilateral and the contralateral eye. For the majority of cells the change in stimulus velocity resulted in a change of directional selectivity; some cells even changed their preference to the opposite direction. The broad velocity-tuning and vigorous responses to moving stimuli indicate that the parabigeminal neurons may modulate the movement-specific activation of superior collicular cells.

◆ **An analysis of the visual auras of migraine**

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Approximately 10% of migraine-headache sufferers experience transitory sensory phenomena immediately prior to the onset of headache. These events are most frequently visual. While several detailed individual case descriptions of classic visual migraine 'fortification spectra' exist in the literature (eg Lashley, 1941 *Arch. Neurol. Psychiatr.* **46** 331–339; Grusser, 1992 *Perception* **21** Supplement 2, 37), there has been little attempt to document the full range of visual phenomena experienced either within or across migraine subjects. The limited information that does exist is anecdotal and retrospective. Subjects (neurological diagnosis: migraine with aura) are trained to make structured observations of their aura episodes as they progress, detailing basic features of the aura including onset and termination times, affected visual field, nature of positive visual elements (line segments, spots, etc), presence of motion and flicker, colour and contrast polarity of positive elements.

Our results to date are based on twelve subjects followed for a period of several months (maximum number of episodes twenty-two). Aura duration varies considerably both across subjects and across episodes. Both positive and negative (scotoma) phenomena are common—individual subjects may experience only positive, only negative, or both sequentially and this may vary across episodes. The positive phenomena seen by an individual also vary across episodes; eg one subject reported bright line elements in seventeen of twenty-two episodes and a variety of other positive visual phenomena in the remaining five. Bright line elements and dots are reported much more frequently than either dark elements or the presence of colour, although reports of both do occur. A variety of other visual observations, including pure motion and 'kaleidoscoping' or fracturing of the visual field, are described. These findings are discussed in terms of possible cortical and subcortical neural substrates, and their implications for the 'spreading-depression model' of aura etiology will be considered.

◆ **Saccadic-eye-movement performance of dyslexic and normal reading teenagers in noncognitive tasks**

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We present the data from sixteen dyslexic and fifteen control teenagers (aged 13–17 years), who were tested with the same psychometric test battery and noncognitive oculomotor tasks as a previous group of twenty-nine children (aged 9–11 years) (Biscaldi et al, 1993 *Perception* 22 Supplement, 19). Saccadic eye movements were measured in the single-target-overlap task (target appears randomly 4 deg to the left or right of the fixation point, which remains visible) and in sequential tasks (five targets appear sequentially from left to right). As in the earlier study, the dyslexic subjects were divided into two groups, on the basis of the results obtained in the psychometric test battery: a rather homogeneous group (D2) with no attention or memory deficits and no auditory-discrimination impairment accompanying their reading and writing disability was distinguished from a group (D1) with various cognitive deficits but normal intelligence. A discriminant analysis carried out on six eye-movement parameters from the overlap task differentiated between the control and the dyslexic groups and confirmed the distinction between D1 and D2. The oculomotor data of D1 and D2 differed from those of the control group in the same characteristic way already found for the respective groups of dyslexic children—group D2 exhibited shorter saccadic reaction times with an increased number of express saccades and undershoots. Subjects of group D1, on the other hand, produced larger standard deviations of the saccadic reaction times, longer correction times, and an increased number of anticipatory saccades. In the sequential tasks, group D2 made more saccades and showed shorter fixation durations than the controls; furthermore, the number of backward saccades (regressions) was increased. The dyslexics' oculomotor behaviour is discussed in terms of cortical control over the saccade system.

◆ **GABAergic and glycinergic blockade does not eliminate the potentiating effect of APB on the ERG OFF-response**

E Popova, P Kuppenova, L Vitanova, L Mitova (Department of Physiology, Medical Faculty, 1431 Sofia, Bulgaria)

The effect of 200 μM APB on the ERG OFF-response (d-wave) was investigated in superfused frog optic cups under different conditions of light stimulation, favouring the response either of rods or of cones. APB caused a marked potentiation of the d-wave amplitude and abolition of the b-wave. The effect did not depend on photoreceptor input. The blockade of the GABAergic synapses by 50 μM picrotoxin or of glycinergic synapses by 50 μM strychnine in optic cups untreated with APB potentiated both the b-wave and the d-wave amplitude. The application of APB once the effect of blockers had fully built up caused an additional increase of the d-wave amplitude. In dark-adapted optic cups (conditions favouring the response of rods) this additional potentiation was exactly the same as that obtained in optic cups superfused with APB only ($233 \pm 33.51\%$). In optic cups stimulated with red test stimuli on a blue background (conditions favouring the response of cones) the potentiating effect of APB on d-wave amplitude after glycinergic blockade was the same as but after GABAergic blockade was smaller than that observed in optic cups treated with APB only. In some experiments the optic cups were perfused first with APB and then the blockers were added to the perfusate. The potentiating effect of APB on d-wave amplitude persisted during GABAergic and glycinergic blockade. Our results indicate that the potentiating effect of APB on the ERG OFF-response does not depend on photoreceptor input and is not eliminated by blockade of GABAergic and glycinergic neurotransmission in frog retina. A direct action of APB on mechanisms generating the ERG d-wave is suggested. In light-adapted eyes, in addition to this direct action, some disinhibition from suppressive influences coming from ON-channels through GABAergic interneurons to OFF-channels might contribute to the potentiating effect of APB on the ERG OFF-response.

◆ **Intrinsic connections of the central visual field projection area in striate cortex of the cat**
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Small iontophoretic injections of the retrograde tracer, horseradish peroxidase, were made in the electrophysiologically identified projection area of the central visual field in area 17 of the cat and the region containing labelling was reconstructed in three-dimensional space. The spatial configuration of the labelled zone on the surface of area 17 was asymmetric to the injection site and elongated in the area 17 site at right angles to the area 17/18 border. The extent of the longer axis of the labelled zone (4–6 mm) approximately corresponded to the

diameter of the convergence window reported by Salin et al. The labelled cells (pyramidal and nonpyramidal types) were found in all layers, although the maximum labelling density was in the superficial layers. It is known that intrinsic and extrinsic labelling in area 18 extends further in the anteroposterior than in the mediolateral direction. It is suggested from the present results that the intrinsic labelling pattern is different for the central projection region of area 17 from that of area 18. It is supposed that the well-known differences in functions of these cortical areas are based on the structural peculiarities.

◆ **Hemispheric asymmetry in recognition of emotional facial affect in normal and depressed persons**

E S Mikhailova (Mental Health Research Centre, 34 Kashirskoe shosse, 115522 Moscow, Russia)

The recognition of emotional facial affect was studied in fifteen right-handed healthy subjects and twenty-seven unmedicated right-handed depressed patients, fifteen of them with major depressive disorder (MDD) and twelve of them with schizotypal personality disorder (STPD). Drawings of sad, neutral, and happy faces (size 6 deg), followed by a masking stimulus, were presented in a random sequence to the right or to the left hemifield of vision. The healthy subjects showed a tendency to right-hemisphere advantage in recognition of all types of facial stimuli, but statistically significant interhemisphere differences were revealed for recognition of happy faces only. Depression evoked a worsening of recognition of emotion, most prominently in the MDD group. The MDD patients showed impaired recognition for sad and for happy expressions in the left hemifield ($p < 0.001$) and for sad faces in the right hemifield ($p < 0.005$). The STPD patients showed less-significant impairment: recognition of emotion was disturbed in the right hemifield for sad expressions only ($p < 0.05$). No depressed patients showed any clear hemispheric differences in the emotion-recognition process. The results obtained suggest a slight right-hemisphere advantage in the recognition of emotion in healthy subjects, and absence of hemispheric differences in depression. The side on which recognition of emotion was not affected depended on the origin of depression (MDD or STPD).

◆ **Effects of zatebradine on temporal properties of the ERG response in cats and monkeys**
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The light response of retinal rods is accelerated by the existence of a mechanism which involves the activation at the inner segment of a membrane current (I_h) activated by hyperpolarisation, which in turn speeds up the decay of the membrane potential. In this way the duration of the response to a single flash is shortened. The I_h can be selectively blocked by zatebradine (obtained from Dr Karl Thomae GmbH), a drug known to produce bradycardic effects on the heart. Patients treated with this bradycardic compound report a number of visual effects that could be explained by a reduction of the temporal resolution of the visual system. In order to test the effect of the drug on the visual system we have measured the ERG response in cat and monkey. The stimulus consisted of a full-field sinusoidal modulation of luminance at different temporal frequencies and different conditions of adaptation. The response consisted of a distorted waveform of which we measured the first and second harmonic component. The first harmonic is assumed to reflect the activity of photoreceptors and second-order retinal neurons, while the second harmonic is attributed to the ganglion-cell layers. In cats, where the ERG response is mainly due to the rod system, we observed that the cutoff response frequency was halved by a dose of zatebradine of 0.5 mg kg^{-1} , while the second harmonic was almost unaffected. Similar results were also obtained in monkeys where the effect of the drug was particularly prominent at low mean luminance levels of the stimulus. These results are consistent with the idea that the main action of the drug measured at the ERG level is on the rod system, and may explain the visual disturbances reported by patients treated with the bradycardic drug.

POSTERS: SECOND SESSION

EARLY VISUAL PROCESSING I

◆ A short sharp shock: perceived edge blur in two-dimensional images

M A Georgeson, T C A Freeman (Department of Vision Sciences, Aston University, Birmingham B4 7ET, UK)

We examined the perception of edge blur for edges of different lengths, in order to derive the two-dimensional characteristics of local spatial operators that serve blur encoding. We showed previously (Georgeson and Freeman, 1993 *Perception* 22 Supplement, 21) that, for long one-dimensional edges, perceived blur (evaluated by a blur-matching method) could be very well predicted if edge blur was encoded as the square root of the ratio of the first to third spatial derivatives taken at the edge point, in a direction orthogonal to the edge. Thus for a vertical edge, $L(x)$, located at $x = 0$, the blur code is given by $[-L'(0)/L'''(0)]^{1/2}$, where ' denotes partial derivative $\partial/\partial x$. We have now found that perceived blur depends on the length of the edge, implying that the first and third derivative operators (denoted D1 and D3) have appreciable extent in the y-direction. For a fairly blurred test edge (blur sd = 11.3 min arc) the matching blur of a long comparison edge fell by a factor of nearly two as the test length was decreased from 240 min to 7.5 min. That is, short blurred edges look sharper than long ones. Perception of fairly sharp edges (sd = 2.8 min) was almost unaffected by length. The blurred-edge data are nicely explained by assuming that the D1 operator is about 3 times longer than D3 in the y-direction. For the 11.3 min test blur, D3 must be about 20 min arc in length, while D1 is about 60 min. Results were very similar when we compared single test edges of various lengths H with long edges whose contrast was reversed every H min arc in the y-direction. This implies that the D1 and D3 operators have nonlinear spatial summation along their length. One attractive interpretation is that the operators add the responses of a set of small subunits distributed in the y-direction, after half-wave rectification of the output of each subunit. This would yield length summation along like-signed edges, but would prevent cancellation by abutting edges of opposite sign. Further data from compound gratings and plaids are consistent with this general model.

◆ Flicker sensitivity as a function of target area with and without external temporal noise

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Retinal receptors and neural visual pathways filter temporal visual signals and noise before they are interpreted in the human brain. On this basis, we modelled the human foveal visual system as a signal processor comprising (i) low-pass filtering due to the modulation transfer function (R_{MTF}) of the receptors, (ii) high-pass filtering (lateral inhibition) due to the modulation transfer function (P_{MTF}) of the visual pathways, (iii) addition of internal neural noise, and (iv) detection by a local matched filter. We used a two-alternative forced-choice method and measured flicker sensitivity as a function of temporal frequency of 0.5–30 Hz for target areas of 0.307–78.5 deg² and rms noise contrasts of 0 and 0.15. Without external temporal white noise, flicker sensitivity had a band-pass shape as a function of temporal frequency. In addition, flicker sensitivity increased with the area. In temporal noise, flicker sensitivity decreased monotonically with increasing temporal frequency. It was independent of target area. In double logarithmic coordinates, efficiency of detection decreased as a linear function of flicker frequency. R_{MTF} could be described as a low-pass Butterworth filter while P_{MTF} was found to be directly proportional to temporal frequency. The spectral density of internal neural noise was found to be independent of area. At the temporal frequencies and target areas used, our model explained about 95% of the total variance of the experimental flicker-sensitivity data.

◆ The sensitivity function to Gabor stimuli (GSF): the relation between GSF and CSF

J M Artigas, J Malo, A Felipe, A Pons (Departamento di Optica, Facultat Ciencias Fisicas, Universitat de València, València, Spain)

Gabor functions form a complete basis in $L^2(R^2)$. This fact enables us to characterise a two-dimensional linear processor by means of a function representing how the system attenuates each element of the chosen Gabor basis. We use the term Gabor sensitivity functions (GSF) for the attenuation function for Gabor stimuli in the human visual system. In addition to the advantages of a coding system based on functions localised both in the spatial and in the frequency domain, the hypothesis that images are coded in the cortex according to their Gabor transform (GT) coefficients at an early stage of the visual process is supported by physiological evidence.

Thus it is quite natural to assume that the preprocessing of visual information is performed by means of a GSF, selectively favouring certain input image GT components.

In this work we show a relation between the GSF and the CSF. To do this we take advantage of the properties of both Fourier and Gabor bases, and assume they each adequately characterise the system. The expression so obtained allows us to compute the GSF from the numerous extant references about the CSF. In the same way, we can calculate the CSF from measures of contrast sensitivity to Gabor stimuli, more and more frequently found in the recent literature. Comparison of the results obtained with each method will provide information about which Gabor channels are actually used by the visual system and, thus, where to look for interaction between channels.

◆ **Contrast-sensitivity measurement: a new method for high spatial frequencies**

V Dubrovskii (Laboratory of Perception, Department of Psychology, Moscow State University, 103009 Moscow, Russia)

A quantitative model of the visual system based on the modulation transfer function (MTF) fails to predict the contrast-detection thresholds for every test pattern with reasonable exactness. A plausible explanation is that the MTF is usually considered to be proportional to contrast sensitivity to sinusoidal gratings, which must be measured over a wide spatial-frequency range. The commonly employed television technique makes possible precise determination of threshold contrasts only for relatively low (20 cycles deg^{-1} and under) spatial frequencies, because the spatial-frequency response of the monitor rolls off at high frequencies. Neglect of this factor may introduce large errors into the measurement. To circumvent this difficulty, a new efficient technique has been developed for direct measurement of the Michelson contrast of a grating presented on the screen. This method allows us to account for the MTF of the monitor automatically. We use a photomultiplier with the high-resolution optical system positioned so as not to impede the subject. This equipment ensures quick measurement of the luminance at the specified point on the screen during the experimental session. The subject's task is to adjust the displayed grating contrast to the threshold. Then the control computer moves the grating on the screen to measure the brightness of its minimum and maximum by means of a photomultiplier. The whole procedure takes about 30 s. In very few experiments described by other authors were measurements of the high-frequency range performed. In these works, contrast thresholds for high-frequency gratings measured by the television technique are approximately 4–5 times as high as those obtained in our experiments: around 2%–3% for 25 cycles deg^{-1} , 4%–7% for 30 cycles deg^{-1} , 7%–12% for 35 cycles deg^{-1} for different subjects. On the other hand, these data are in agreement with those measured with optically generated gratings. It is concluded that the spatial-frequency band of the visual system is wider than was believed so far.

◆ **Influence of background structure on local orientation discrimination in early vision**

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In earlier experiments it has been demonstrated that a line segment can be detected among distractors of different orientation by a fast 'preattentive' process (Julesz, 1975 *Scientific American* 232(4) 34–43). Such a performance is assumed to involve filter mechanisms acting in parallel over the visual field (Foster, 1991 *Proceedings of the Royal Society of London, Series B* 243 75–81). We wanted to know how the degree of activity of these filters can interfere with orientation discrimination. Precisely, does orientation information, extracted from the background, improve or hinder orientation discrimination of a line target? In a two-alternative forced-choice task observers had to discriminate the orientation of a line segment at threshold presented centrally within a background composed of line segments with orientation either the same as or opposite to that of the target ($+45^\circ$ or -45°). The results show that discrimination performances are improved when the background and the target have the same orientation, and diminished when they have opposite orientation. To test whether these findings still hold when more than one orientation is present in the background, we ran a second experiment. An orientation (horizontal and vertical, tilted at $+45^\circ$ or -45°) was randomly assigned to each segment in the background and the number of segments of each orientation was varied. The luminance of one oblique segment, randomly chosen, was decreased during the 30 ms before the whole display was switched off. The task of the observer was the same as in the previous experiment. The results show that discrimination performances are improved when the structure of the background provides less information about the target orientation (the number of segments of the same orientation as the target was decreased). These findings suggest that the processing of orientation in a nonhomogeneous background affects orientation discrimination of a local target presented within that background.

◆ **Interactions in space and time between the visual responses to two brief lines**

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The Rashbass model [Rashbass, 1970 *Journal of Physiology (London)* **210** 165–186] for detection of temporal events was applied to study the spatiotemporal interactions between the responses to two brief lines. The model consists of a linear filter with a spatiotemporal impulse function, which is assumed to be a harmonic wave function modulated by a Gaussian function (Manahilov, 1992 *Perception* **21** Supplement 2, 82). It is followed by a nonlinear process, which integrates the squared neural response over time and space, thus yielding the total energy of the neural response. The contrast threshold is reached when the total neural energy attains some constant criterion value. Two brief lines were presented foveally either at the same place at various stimulus asynchronies or simultaneously at different distances. For each experimental condition the detection thresholds of eight stimulus configurations (specified as points at an interval of 45 deg in a two-dimensional coordinate system whose axes represent the contrast and polarity of each stimulus) were measured. Each set of results was fitted by the equation of ellipse. Thus, the temporal and spatial autocorrelation functions of the spatiotemporal impulse response were evaluated. The spatiotemporal interactions were characterised by summation at short asynchronies (0–30 ms) and small distances (0–2 min arc) as well as by inhibition at longer asynchronies (60–80 ms) and larger distances (4–8 min arc). The temporal and spatial autocorrelation functions, calculated by the spatiotemporal model of contrast detection, fitted well to the data obtained. Moreover, the predicted spatial transfer function for briefly presented stimuli exhibited a good agreement with the spatial-frequency contrast-sensitivity function measured with briefly presented gratings. The calculated temporal transfer function for a line also gave a good fit to the temporal-frequency contrast-sensitivity function estimated by a line stimulus.

◆ **Spatial integration in orientation discrimination**

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Orientation-discrimination thresholds were measured with cosine gratings of various areas and spatial frequencies in the presence of two-dimensional external spatial noise. A two-alternative forced-choice method was used, and the observers were asked to indicate which one of the two successive stimulus exposures contained a grating rotated anticlockwise; the other exposure always contained a vertical grating. To evaluate the human ability to integrate image information across space we compared the results with those of an artificial observer that collected image information without any limitation in spatial extent. The artificial observer is identical with the difference between the rotated and vertical gratings. Its response was computed as the correlation between the artificial observer and the stimulus. Human efficiency was computed as the ratio of signal-to-noise ratios (d') of human and artificial observers at the human orientation threshold. Human orientation threshold decreased with increasing stimulus area, but the thresholds for artificial observers decreased even more. Therefore, human efficiency decreased with increasing stimulus area, which means that a progressively smaller proportion of image information is used as stimulus area increases. The decrease of efficiency was scale invariant: efficiencies were nearly identical when the number of square cycles was equal at the spatial frequencies studied ($1-8$ cycles deg^{-1}). Therefore, a magnification or minification of a stimulus does not affect orientation-discrimination performance. The present findings, in agreement with contrast-detection studies, support the view that, probably owing to attentional limitations, the collection of image information becomes less accurate as the number of details (square cycles in this case) in the image increases.

◆ **The apparent fineness of peripheral gratings does not depend on their luminance or duration**

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As a general rule, any manipulation of contrast, luminance, orientation, duration, and eccentricity which takes a grating closer to its detection threshold also increases its apparent spatial frequency (Georgeson, 1980 *Philosophical Transactions of the Royal Society, Series B* **290** 11–22). This has been explained in terms of tuned spatial-frequency channels which alter their receptive-field properties but retain their size labels. At lower luminances, for example, the optimal stimulus for a given receptive field becomes larger (as surround inhibition reduces), whilst its label remains the same. However, it is not clear, on this account, what purpose is served by having a permanent difference in the apparent sizes of foveal and peripheral stimuli.

An explanation may lie in the changing ratio of M and P cells with eccentricity (Perry et al, 1984 *Neuroscience* **12** 1101–1123). It seems possible that some aspect of the conditions generally used to measure apparent peripheral spatial frequency unfairly favours the fovea. In a method of constant stimuli, six subjects matched the apparent spatial frequency of a 1 cycle deg^{-1} foveal grating to that of a similar grating 9 deg into the periphery, at two luminances (35 and 1600 cd m^{-2}) and two presentation durations (1000 and 150 ms). Probit analysis of the data confirmed an increase in apparent spatial frequency of peripherally viewed gratings, but the size of the effect was very similar in all four conditions (mean peripheral increase \pm SE: high long $8.2\% \pm 2.56\%$; low long $8.4\% \pm 2.14\%$; high short $11.1\% \pm 2.56\%$; low short $9.6\% \pm 3.06\%$). Thus substantial changes in both luminance and presentation duration, which are known to affect M and P cells differentially, had no significant effect on foveal/peripheral differences in apparent spatial frequency. The origin of the observed anisotropy between fovea and periphery remains obscure.

◆ **Motion-contrast acuity and retinal eccentricity: a comparison of psychophysical and VEP measures**

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We investigated the effects of retinal eccentricity on motion-contrast 'acuity' and VEPs. For this purpose, eight subjects were presented with a form-from-motion Landolt ring at retinal eccentricities of 0, 2, and 5 deg in the left visual hemifield. The observers had to indicate one of four possible positions of the gap in the ring. During stimulus presentation, VEPs were recorded at Oz, O1, and O2. Acuity (measured as percentage correct) was significantly poorer when stimuli were presented in the periphery. Analogously, the amplitudes of the prominent VEP components N2, P2, and N3 were significantly reduced. VEP latencies did not vary with stimulus eccentricity. N2, P2, and N3 amplitudes were highly and positively correlated with the acuity measure (correlations between 0.66 and 0.95). The slopes of the acuity and N2-amplitude functions were proportional to the magnitude of the 'cortical magnification factor', as quantified by Rovamo and Virsu (1979 *Experimental Brain Research* **37** 495–510). The N2 amplitudes at Oz, in particular, were almost perfectly fitted by their equations. Thus, motion-contrast acuity appears to depend upon the magnitude of the cortical reference area in V1. The implications of these findings are discussed.

◆ **Perceived size distortions in a bisection task**

A Bertulis, A Bulatov (Kaunas Medical Academy, Mickevichaus 9, 3000 Kaunas, Lithuania)

We have devised experiments to measure size illusions induced by a single masking line in a bisection stimulus. Before the experiments we tested subjects' ability in spatial-interval discrimination. Three vertical lines, each 0.4 min wide and 14 min in height, were generated on a monitor. Subjects were asked to make the two spatial intervals equal by pushing one of the flanking lines to the left or to the right. Absolute error value increased from 0.1 to 2 min with interval sizes varying from 4 to 70 min. In the experiments we measured the accuracy with which the subjects judged two intervals as equal, with a masking line (vertical, size 0.4 min \times 14 min) present within one of the intervals. The perceived length of the masked interval was distinctly different from that of the unmasked one. Illusion-strength value was measured as a function of (i) the size of the bisection stimulus, (ii) the position of the masking line in an interval, and (iii) the position of the masked interval—situated on the left or on the right side. The absolute value of the illusion increased regularly from 1 to 10 min with interval size varying from 4 to 70 min. Maximum values were found with the masking line situated in lateral half of an interval and changing its position with stimulus size. Left-right asymmetry, if any, was negligible. The data obtained suggest that size illusion in a bisection task is mediated by spatial-filtration processes and provide corrections of cortical-filter characteristics in a computational model: (a) the chi-square (Rayleigh) law should be applied for distribution of receptive fields of different size, and (b) gaze fixation should not be ignored. The results of our psychophysical study fit well with the neurophysiological findings (Dow et al, 1981 *Experimental Brain Research* **44** 213–228).

◆ **The behaviour of the neural CSF in the low-spatial-frequency range**

A Felipe, J M Artigas, P Capilla, M J Buades† (Departamento de Optica, Facultad Ciencias Físicas, Universitat de València, València, Spain; †H Virgen de la Arrixaca, Murcia, Spain)

The generation of interference patterns on the retina to estimate the retina-brain contrast sensitivity implies the use of coherent light. The function so obtained is usually called the

neural contrast-sensitivity function (CSF). Since there are no diffusers in the apparatus and so there is no speckle, the masking effect produced by this spatial noise does not appear. We know that the neural CSF presents greater sensitivity than the incoherent one as there is no attenuation due to the optics of the eye. Notwithstanding, the results for the low-frequency range are confusing, owing to the instability of interference patterns in this range that makes measurements difficult. On the other hand, with these devices the contrast was changed by reducing spatial coherence (adding incoherent light) or temporal coherence (changing the temporal signal overlaps). Thus, measuring the CSF in this way, we change from using highly coherent light for the high-frequency range to using nearly incoherent light in the low-frequency range. In this work, we study the behaviour of the neural CSF in the low-spatial frequency range. To this end we use a Maxwellian vision system that forms the image of a grating of fixed frequency and contrast directly on the retina, using as light source a He-Ne laser. This device is analogous to the interferometric one, but it does not present any kind of instability in the low-frequency range, and neither is a loss of coherence needed to reduce the contrast. The results show a marked sensitivity loss in the low-spatial-frequency range. This is caused by the masking effect by spatial noise generated inside the eye. The noise arises from local inhomogeneities in the optics, mainly at the surface of the cornea, where the largest change in refractive index occurs en route to the photoreceptors. This noise appears coarse and accounts for the fact that its spectrum contains mostly low spatial frequencies.

◆ **Accommodation response and mental task**

A Kurtev, B Stoimenova, M Georgiev (Department of Physiology, Faculty of Medicine, Medical Academy, 1431 Sofia, Bulgaria)

The effects of mental tasks on accommodation have been studied by many authors, often producing conflicting results (Gawron et al, 1985 *Aviation, Space, and Environmental Medicine* 56 225-232; Kruger, 1980 *American Journal of Optometry and Physiological Optics* 57 440-445). Such studies have concentrated either on tonic accommodation or on no more than three values of accommodative effort. We measured accommodation response at five different levels of vergence while subjects performed different mental tasks—counting, simple arithmetic, and undemanding visual-acuity discriminations. The accommodative stimulus was provided by a pattern positioned at infinity in a Maxwellian system and viewed monocularly through negative lenses of different power placed in front of the left eye. Accommodation was measured objectively in the other eye with a Hartinger optometer. The experiments were performed in three sessions encompassing six different series. We studied ten young subjects whose accommodative range expanded beyond the maximum accommodative effort required (4 D). Not all subjects were able to perform all series of the experiment successfully and one subject failed altogether to maintain a sustained response. The results showed that performing a mental task while accommodating to a stimulus may have different effects on accommodative response. Half of the subjects exhibited no obvious changes in relation to the mental task. In three subjects the mental task significantly affected the lowest accommodative effort without changing the rest of the curve. In some subjects, while performing mental tasks there was a trend for a less effective accommodation response, as in a deteriorating visual environment, but the changes were not significant. The results suggest that mental tasks may influence accommodation response through different mechanisms, and therefore different subjective metrics of mental load should be applied in order to quantify the effect.

◆ **Geometrical illusion as a difference in the perceived size between the two eyes**

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Two halves of a Müller-Lyer figure are generated on a monitor and presented separately to the left and the right eye of a subject. Subjects report the two figures joining together owing to fusion of their medial wings, which have the same shape, size, and orientation. Under these circumstances, the united Müller-Lyer figure is as clearly visible as when it is viewed either monocularly or binocularly. There is evidence that the fusion effect is provided by stable fixation of the two foveas on identical images reducing them into a single segment of perceived figure. In our experiments the illusion is as strong as that reported recently (Bulatov et al, 1993 *Perception* 22 Supplement, 128). Nevertheless, the illusion as a function of tilt angle of the wings (0° to 180°) has a quite symmetrical shape with the zero value at 90° of tilt angle and equal maxima on both sides. This makes the function different from that obtained monocularly when individual variations of asymmetry arise, since gaze fixation changes from subject to subject. In the present study a distinct asymmetry of function is observed only in patients having refraction differences between the two eyes. A dissimilarity such as 0.25 diopter results

in 6° – 10° shift of the zero point of the curve and 10–16 min arc difference between the illusion-strength value on the left and the right sides. Neurophysiological interpretation of the data obtained and modelling confirm the suggestion that the Müller-Lyer illusion results from visual-information processing at the retinal-cortical network level rather than from psychophysical functions at higher sensory levels. The fusion effect observed provides a gaze-fixation method in psychophysiological measurements. Under the given experimental circumstances the method may also be used for testing of visual-acuity differences between two eyes.

◆ **Relative, not absolute, luminance determines processing time**

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Simple reaction time is known to decay as a hyperbolic function of luminance (Piéron's function). It has also been shown recently (Pins and Bonnet, 1993 *Perception* 22 Supplement, 127) that the same relationship exists between choice reaction time and luminance. In this study, we addressed the question of the factor that could explain this observation. Our assumption, inferred from a generalisation of Link's model [1992 *The Wave Theory of Discrimination and Similarity* (Hillsdale, NJ: Lawrence Erlbaum Associates)], is that relative and not absolute luminance determines processing time. Since it is known that Weber's ratio increases near threshold, it would be expected that multiple functions could fit the data of a reaction-time experiment with a wide range of luminance levels starting at threshold. If, on the other hand, absolute luminance were responsible for the decrease in reaction time with increasing luminance, a single function would be predicted. We tested this assumption in a discrimination experiment (two-alternative forced-choice method) with a large range of luminance levels from just below threshold to mesopic intensities. The results show that multiple functions fit the data and that their exponents vary with the range of luminance taken into account. The more this range approaches the absolute threshold level, the higher are the exponents of the chronometric functions. Our results also suggest that the exponents become stable when the range of luminance approaches mesopic levels. The observations indicate that relative, not absolute, luminance determines the decrease in processing time with increasing luminance of the stimulus. This interpretation is confirmed by the results of a control experiment where we varied background luminance.

◆ **Structural aspects of visual masking: what determines masking efficiency?**

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Previous experiments (Delord and Bonnet, 1993 *Perception* 22 Supplement, 127) showed that masking effects depend mainly upon target visibility. Consequently, a semiquantitative analysis of the structural proximity between target and mask, achieved by computing the difference between the 2D-FFT amplitude spectra (target spectrum minus mask spectrum), had provided a first description of the visible structure of the target remaining after the presentation of the mask. If masking efficiency depends on the relative visibility of the spatial-frequency bands of the target, it is then expected that manipulation of the noncritical spatial-frequency content of the target, with regard to the task, should not lead to a difference in masking efficiency. Two trained observers were asked to discriminate the global orientation (oblique left, oblique right) of a texture bar followed by either a 'pattern' mask or one of three 'noise' masks whose element size differed. Targets and masks were composed of the same textures. The results show that the most efficient mask was not necessarily the one with the same texture as the target but rather the mask containing the highest amount of energy in the low-spatial-frequency ranges, in all stimulus conditions. Our findings therefore suggest that masking effects are related to visibility. They are thus predictable in the spatial-frequency domain, taking into account the relevant spatial-frequency bands of the target for the particular task. The data suggest that the functional distinction between 'pattern' and 'noise' masks (Turvey, 1973 *Psychological Review* 81 1) might therefore result from an inaccurate and/or inadequate definition of structural similarity.

◆ **Visual discrimination of line length and tilt: psychophysical characteristics of response distributions**

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Essential psychophysical features of visual discrimination are revealed by examination of response distributions for shape and slope in different parts of a near-standard region. The issue was studied by using two kinds of spatial stimuli: line length and tilt. In a visual-adjustment task observers worked in different parts of the region (between the lower and

upper just-noticeable-difference points) according to instructions. For both stimuli, response-frequency distributions were symmetrical and equally variable in the whole region (where the line-length problems had not previously been examined). Line-tilt data may be explained by the basic psychophysical assumption (based on Stevens's subjective-scaling results): line tilt can be considered as a 'metathetic' kind of stimulus in which one sensation value is substituted for another when a stimulus value changes. Therefore variability of responses (and their distribution characteristics) may remain constant in the region examined. The analogous character of line-length distribution may indicate the 'substitutional' process in the region as well. Distributions obtained here are similar to those for another 'metathetic' visual feature—hue. In contrast, steeper or asymmetrical curves at the region borders were found for a 'prothetic' feature—brightness (caused by a probable 'additive' elevation of sensation value when a stimulus difference increases). These data and those of other authors show that the 'substitutional' process of line-tilt discrimination may be based on (a) absence of a monotonic decrease in discrimination when a stimulus value increases, (b) well-known neuronal-detector mechanisms, and (c) constancy of response distributions in the region considered. In distinction, the 'substitutional' process for line length is indicated by (b) and (c), whereas the 'additive' process is indicated by a monotonic decrease in discrimination when a stimulus value increases. Line length may belong to an 'intermediate' stimulus class (proposed to involve scaling). In general, the dichotomy of 'substitutional' and 'additive' processes remain debatable.

◆ **Modeling for amplitude discrimination of visual signals**

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Mathematical aspects of amplitude discrimination of visual signals on a random-noise background are considered. The 'observer' is supposed to have a two-dimensional sensitivity function $A(x)$ and internal noise, consisting of two components (independent of and dependent on the input signal). The signals in the series are assumed to have the same normalised luminance distribution $l(x)$ ($0 \leq l(x) \leq 1$), but different amplitudes L and $L + \Delta L$. The task of the 'observer' is to decide whether the signal amplitude under analysis equals L or $L + \Delta L$. This task is equivalent to the visual detection of the amplitude difference ΔL for the same signal shape $l(x)$. The detectability index d' is used as the measure of a distance between two distributions of the decision variable for the 'observer' that correspond to the two types of input signals. The 'observer' is supposed to choose the optimal $A(x)$, maximising the value of d' . The original technique for the analytical solution of optimisation problem $d' \Rightarrow \max$ is proposed. The main result is that optimal function $A(x)$ for maximisation of d' is not only dependent on the signal shape $l(x)$, but also on mean background luminance L_0 and the internal/external noise ratio as well. The numerical calculations for $A(x)$ and d' as a function of the signal-to-noise ratio on the input image, internal/external noise ratio, value of ΔL , and shape $l(x)$ of a signal were made. It was shown that optimal function $A(x)$ should consist of two (positive and negative) parts. Moreover, the spatial size of the positive part for a fixed value of d' increases if the mean luminance L_0 decreases, and vice versa. These results correspond well to the plasticity of the receptive-field-centre size as well as to the perceptive-field size in human observers under variable L_0 .

◆ **Does saccadic suppression selectively inhibit the transient response?**

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A stimulus appears longer in duration when it is presented during a saccade than when presented during fixation. We conducted experiments to determine the difference in perceived duration of a stimulus in these two cases. A small red light 30 min in diameter was presented on a 45 deg \times 60 deg white background field. The stimulus was presented for 80 ms just after the end of a saccade, and it was presented again with 570 ms of interstimulus interval while the observer was fixating. The duration of the second presentation varied in every trial in a staircase manner. The observer judged which stimulus appeared of longer duration. The results show that the first, 80 ms, stimulus matched in perceived duration the second stimulus at 120 ms. We performed further experiments with a hue-substitution stimulus. A small red light replaced a green steady light of the same size presented on the white background. In this condition, the first stimulus matched the second stimulus in perceived duration when their physical durations were the same.

It is generally accepted that the visual system has several subchannels which have different temporal properties. The response to the red luminance-increment stimulus may consist of

transient and sustained components. If saccadic suppression selectively inhibits the transient component, the observer can use only the sustained component to evaluate the duration of the stimulus. As a result, the stimulus appears longer under saccadic suppression than during fixation, when both the transient and the sustained channel can work. The isoluminant stimulus used in the second experiment may be undetectable by the transient channel. Therefore saccadic suppression has no effect on the isoluminant stimulus.

◆ **Non-Fourier channels in stereopsis and motion**

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When images of two or three sinusoidal gratings with nearby frequencies are viewed, either binocularly or drifting in time, the (non-Fourier) beats are often perceived somewhat independently, as a form of multiplicative transparency. With drifting gratings, the beats can appear to drift in front of a stationary carrier (or fine structure). With binocular viewing one can use nearly horizontal sinusoids so that the beats are vertical with a nonzero binocular disparity, while the carrier is horizontal and manifests no disparity. In this case, one can perceive the beat structure floating transparently in front of the fine structure. This effect is stronger if one makes the multiplicative beat more like a square-wave by adding a third harmonic.

We also consider whether the beat is extracted from a channel that is not orientation-specific (Chubb and Sperling, 1988 *Journal of the Optical Society of America A* 5 1986-2007) or after oriented filtering (Wilson et al 1992 *Visual Neuroscience* 5 79-97). If the beat arises from an orientation-specific channel, then this implicates horizontally tuned channels in binocular processing. Subjects were adapted to a high-contrast grating, which was followed by a brief presentation of a low-contrast carrier/beat pattern composed of sinusoids with nearly horizontal orientations, so that the beat is vertical and the carrier is horizontal. We find that adaptation to the beat orientation (vertical), either at the beat wavelength or the carrier wavelength, does not affect the discrimination of the vertical beat. Adaptation to the carrier orientation (horizontal), where Fourier power is concentrated, does affect one's ability to perceive the vertical beat. Our results provide further evidence for the use of (non-Fourier) contrast envelopes in stereopsis, showing that non-Fourier and Fourier information can be perceived independently, as is well known in the case of visual motion. It supports the notion of a postfiltering nonlinearity, in which the non-Fourier beats arise from orientation-tuned channels; these would be horizontally tuned in our binocular case.

DEVELOPMENT AND AGING

◆ **Developmental changes in visual search**

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Previous studies have shown that the ability to segment oriented textures is age dependent (Sireteanu and Rieth, 1992 *Behavioral Brain Research* 49 133-139). In this study, we investigated the role of age in visual search. In visual search tasks, subjects look for a target item among a number of distracting items. If the time required to complete the search is roughly independent of the set size, the search is said to be parallel; if search time increases with the number of distractors, the search is said to proceed serially. Our stimulus displays consisted of complete versus open circles, circles versus circles with an added line, parallel versus converging lines, or vertical versus tilted lines. The set size could be 1, 4, 8, or 16. The items were presented on a computer screen. The subjects' task was to press the button of the computer mouse with the dominant hand as soon as they detected the target, then to indicate with the same hand where the target had been. Each subject performed eight test runs with fifty-six trials, grouped in two experimental sessions. One hundred school children, aged from 6 to 20 years, and twenty naive adult observers participated in our experiments. The basic reaction time gradually decreased with age. For all age groups and all tasks (except stimuli consisting of vertical versus tilted lines), the functions relating search times to set size showed an asymmetry, basically confirming the data presented in previous studies with adult subjects (Treisman and Gelade, 1980 *Cognitive Psychology* 12 97-136). The slope of the search curves decreased with age. Subjects aged from 16 to 20 years performed the tasks more effectively than adult observers. For some subjects, all search tasks, including those which were initially serial, had become parallel with practice. These results indicate that the efficiency (absolute reaction time and slopes) of visual search is age dependent.

LEARNING AND MEMORY

◆ Perceptual learning of colour constancy and the role of illuminant familiarity

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Colour constancy is defined as the invariant appearance of surface colours under changes in the spectral composition of the incident illumination. The ability to identify correctly surface colours may depend in part on the observer's familiarity with the light source. In this study we examine whether practice of judging surface colours under different illuminants leads to an improvement in colour constancy, and, if so, whether the improvement is restricted to the illuminants under which the judgments were made. Five subjects were asked to identify by name (chosen from eleven basic colour terms) a total of seventy colour patches under six different illuminants: one standard 'white' illuminant, three other broad-band illuminants, and two narrow-band sources. Each patch was presented tachistoscopically in the centre of a Mondrian surround. Subjects then named each colour patch a further thirty times distributed over a two-week period, ten times under each of two of the broad-band illuminants and ten times under one of the narrow sources. Finally, subjects again named the patches under all six illuminants. It was found that the degree of colour constancy—assigning the same name to the same colour patch under different illuminants—under broad-band illumination was significantly better after the learning trials, and that the improvement was greater for the illuminants used in the learning trials. However, under narrow-band illumination colour constancy was very poor both before and after the learning trials. It was also found that the samples defined as focal colours under the standard illuminant were more likely to be defined as focal colours under the other illuminants after the learning trials than before them. We are now investigating colour constancy in colour experts (eg paint mixers) and preliminary results suggest that they have superior constancy.

◆ Visual short-term memory in monkeys for different visual attributes: distinctions in cholinergic mechanisms

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Visual short-term memory characteristics were tested in a delayed-discrimination task on rhesus monkeys before and after a systemic injection of the cholinergic antagonist amizil ($0.3\text{--}0.8\text{ mg kg}^{-1}$). Monkeys were trained to discriminate visual stimuli and complicated scenes with different visual attributes (colour, orientation, spatial frequency, size, contrast, etc) during elaboration of a delayed (0–16 s) instrumental reflex. Amizil had no influence upon mechanisms of long-term memory (visual discrimination without delay), but impaired short-term storage of visual information and increased motor reaction times. However, the duration of information storage in the short-term memory of the monkeys for each visual attribute decreased (by a factor of 2) at different doses of amizil. Application of the amizil in a dose of 0.3 mg kg^{-1} produced a different result: strong impairment of delayed discrimination of the black–white spatial-frequency gratings and several complicated scenes, with no changes in short-term storage of form, contrast, orientation, and colour information. The delayed discrimination of form, contrast, and orientation was also impaired after injection of the amizil in doses of $0.45\text{--}0.6\text{ mg kg}^{-1}$. The impairment of delayed discrimination of colour was obtained through an application of amizil in doses of $0.7\text{--}0.8\text{ mg kg}^{-1}$. The results suggest that the short-term-memory system involves many different mechanisms, which are represented in the brain by different neural structures with different organisation of the neuromediator systems. Each such mechanism is specialised for a particular set of visual attributes. In the course of an organism's interaction with its environment, these mechanisms may participate in the retention and use of different kinds of visual information.

◆ Participation of the cortical glutamatergic mechanisms in the visual short-term memory in monkeys

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We investigated the effect of glutamatergic (NMDAergic) suppression, caused by intracortical perfusion of the glutamate antagonist APV (1 mM), on visual recognition and visual short-term memory in rhesus monkey and on the responses of visual and prefrontal cortical neurons. Each animal performed delayed discrimination of coloured visual stimuli before and after an intracortical application of the APV. We used a combination of the microdialysis technique with multichannel recordings from single units (in the immediate vicinity of the dialysis tube) of the monkey cortex. APV had no influence upon mechanisms of long-term memory (discrimination

without delay). The results for short-term memory, obtained with the dialysis tube penetrating the visual and the prefrontal cortex, were different. The APV perfused in the visual cortex considerably decreased the duration of short-term storage of information (by a factor of 2–3) and reliably increased motor reaction times. These behavioural changes caused by the APV were accompanied by activity suppression in 70% of neurons and activity increase in 20% of neurons in the visual cortex. The activity changes were more pronounced at the stage of short-term memory and decisions. The intracortical effect of APV in the prefrontal cortex resulted in less-significant impairment of short-term memory and motor reaction times in the monkey. However, activity increase was correlated with the effect of APV in 65% of neurons in the prefrontal cortex, and 25% of neurons decreased their activity. The results show that cortical glutamatergic mechanisms play an essential role in the system of visual short-term memory and indicate a difference in their functional and structural organisation in the visual and the prefrontal cortex.

◆ **Event-related-potential correlates of unconscious processing and incidental memory**

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Event-related potentials (ERPs) were recorded to complex images composed of attended central figures and unattended eccentrically presented ones. Subjects were 7-year-old children. They had to attend to one (relevant) of four central stimuli and to ignore the others. Eccentric figures (size 5.6 deg, eccentricity 6 deg) not mentioned in instruction were processed unconsciously because of inattention, brief exposure (60 ms), and backward masking. The results of two experimental situations were compared—stable eccentric images, one of which was connected with the relevant central figure and another with the irrelevant ones; and variable eccentric images. With variable eccentric images, ERPs to complex stimuli containing the relevant central figure were characterised by an amplitude increase of P150 in O2, and of P300 in O2, P4, and T4/6, as compared with ERPs with stable lateral images. These data show the role of the right hemisphere in entering stimulus characteristics into working memory. Bilateral changes of P150 and P300 in caudal areas were also observed in ERPs to the isolated presentation of the central relevant stimulus, which was the same in SIS and VIS. The results are interpreted as formation of a 'neuronal model of the situation' which may be characterised by incidental memorising of stimulus features.

◆ **Movement-discrimination learning is impaired in visually deprived cats**

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Three groups of cats were used: cats deprived binocularly of patterned vision from birth (BD cats), control cats reared in the laboratory with opened eyes (C cats), and cats reared in a rural environment during the first month of life (N cats); each group consisted of four cats. The cats were trained in a two-choice discrimination apparatus for food reward. The sessions consisted of sixteen trials. In the first stage of training the positive stimulus was a gate with a moving downward or upward light spot, whereas the negative stimulus was the other blank gate. In the second stage, the negative stimulus was a stationary spot located at the middle of the gate opposite to that with the moving spot. The spot was 2 cm in diameter and the moving spot passed the 37 cm-high gate within 0.8 s. The training was difficult for all groups of cats. However, the BD cats were clearly worst. In the second stage the N and C cats reached the criterion within 10–20 sessions, whereas none of BD cats reached it within 30–40 sessions (the training is being continued). The result is consistent with data from single-cell recording showing a severe impairment of analysis of movement in BD cats (Dec et al, 1976 *Acta Neurobiol. Exp.* 36 687–692). A comparison with previous data from our laboratory (Zernicki, 1992 *Brain Res. Rev.* 16 1–3) suggests that in cats movement-discrimination learning is more difficult than pattern-discrimination learning and that in BD cats movement-discrimination learning is more impaired than pattern-discrimination learning.

◆ **Learning and memory in normal and visually handicapped children**

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The aim in this paper is the longitudinal study of the relationship between academic learning, special curative learning, and memory in sixty-three normal-sighted, fifty-two weak-sighted (corrected vision 1/20–1/10), and sixty-eight partially sighted (vision 1/50–1/20) children. The pupils were classified into age groups: 7–9, 10–12, 13–15, and 16–18 years. The indices of recognition and reproduction of images and visual short-term-memory span were defined by

the method of visual forward and backward masking. Statistical treatment involved Student's *t*-test. It was found that, during academic learning, object recognition improved and short-term-memory span expanded significantly in pupils with normal vision. Those changes were shown to a considerably lesser extent in the weak-sighted and partially sighted children ($p < 0.0002$ and $p < 0.0001$, respectively). In consequence of slow ontogenetic development, image recognition and short-term memory remain at low levels in weak-sighted and partially sighted children even after finishing school. Special curative learning is theoretically founded on a complex system of compensative development of visual perception [1988, *Psikhologicheskii Zhurnal* 9(2) 97-107; 1990, *Zhurnal Vysshei Nervnoi Deyatel'nosti* 40(4) 620-628]. This system includes the following methods: visual rhythmic stimulation, development of visual attention, development of visuo-motor function, and the correction of contrast and chromatic sensitivity, resolution, the visual field, and object recognition. The systematic curative learning during 4 years of a special curriculum was carried out with forty weak-sighted and partially sighted pupils aged 7-9 years. The curriculum promoted development of object recognition and visual short-term memory to a great extent. The short-term-memory span exceeded the corresponding indices in control groups of the same age and older ($p < 0.01$ and $p < 0.05$, respectively). So, longitudinal research revealed considerable capacities for compensation for damage and in development of object recognition and visual memory. These capacities are probably based on the adaptive qualities of brain related to the mechanisms of plasticity. Compensation within the visual system and intersystem, and compensation achieved by the curriculum are very important for overcoming deviations in cognitive development of the low-vision children.

◆ **Recognition of three-dimensional shadow images in Parkinson's disease**

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Previously reported experiments (Lee et al, 1992 *Perception* 21 Supplement 2, 35; 1993 *Perception* 22 Supplement, 107) showed that Parkinsonian subjects tended to make more errors in recognising objects after a 45° rotation than did age-matched controls. They also made increasingly more errors in performing three-dimensional (but not two-dimensional) mental rotation of images (Shepard and Metzler, 1971 *Science* 171 701-703) as the required amount of rotation increased. The results of these two experiments suggest a deficit in Parkinson's disease in the mental rotation of structured three-dimensional shapes.

A subtest of Warrington and James's 'Visual Object and Space Perception Battery' (VOSP) was designed to test recognition of solid three-dimensional objects from their two-dimensional silhouettes. The present test consists of a series of different shadow images, whose recognition was made progressively more difficult by foreshortening their silhouettes. There were two categories of silhouette—household objects and animals. Fifteen Parkinsonian subjects were significantly worse ($p = 0.002$) at recognising the animal silhouettes, and performed as well as the aged-matched controls at recognising the object silhouettes. Results are interpreted in terms of a subtle, category-specific form of visual-object agnosia for novel stimuli that require some form of difficult transformation from two to three dimensions prior to matching with object representations in long-term visual memory.

COLOUR PERCEPTION

◆ **Phenotypes and genotypes of red and red-green hybrid pigments**

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We have investigated thirty-one dichromats with a single pigment gene in the red-green gene array in order to identify red and 5' red-3' green hybrid pigments in vivo and to compare their action spectra with the absorption spectra measured in vitro by Merbs and Nathans for recombinant normal [1992 *Nature (London)* 356 433] and hybrid (1992 *Science* 258 464) human cone pigments. In all the dichromats, exons 2 to 5 have been PCR amplified and sequenced on both strands; and their 2° Rayleigh matches and (16 or 25 Hz) flicker-photometric-sensitivity functions (from 400 to 700 nm) have been measured. Twenty-one of the dichromats have a single normal red-pigment gene, fourteen with R(ser¹⁸⁰) and seven with R(ala¹⁸⁰); and ten have a single 5' red-3' green-hybrid-pigment gene, one with R4G5(ser¹⁸⁰), four with R3G4(ser¹⁸⁰), two with R2G3, and three with R1G2.

In accord with the absorption spectroscopy, we find that the substitution of serine for alanine at position 180 in the red-pigment gene produces a shift of approximately 4 nm to longer wavelengths in the spectral sensitivity of the encoded pigment. Further, we find that the hybrid genes R4G5(ser¹⁸⁰), R3G4(ser¹⁸⁰), R2G3, and R1G2 produced pigments shifted, relative to the normal green pigments, by approximately 6 nm, 4 nm, 0 nm, and 0 nm, respectively. These results establish (i) that there are two classes of deuteranopic and one class of protanopic true reduction-type dichromats with a single normal cone pigment active in the Rayleigh region ($\lambda > 540$ nm); (ii) that there are some reduction-type protanopes with a single pigment active in the Rayleigh region, which is spectrally shifted relative to the normal green pigment; and (iii) that there cannot be a single anomalous pigment common to both protans and deutans or even to protans alone.

◆ **The temporal-frequency response of the early short-wavelength-sensitive cone pathway**

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Violet sinusoidal flicker presented on an intense orange background is detected by S-cones. If the flicker amplitude is modulated at 0.5 Hz, subjects detect a yellowing of the target at the amplitude-modulation frequency. Such a color change is consistent with a compressive non-linearity in the S-cone pathway (Stockman and MacLeod, 1992, ARVO). Subjects differ in their relative sensitivity to the flicker and to the color change, but most subjects detect a color change in the absence of flicker between ~25 Hz and ~45 Hz. We can estimate the frequency response of the S-cone pathway before the nonlinearity by fixing the amplitude-modulation frequency at 0.5 Hz and determining the modulation of the S-cone flicker required to detect the color change as a function of flicker frequency. We have used several methods to measure this function. At frequencies below ~25 Hz, we added an amplitude-modulated L-cone stimulus to the S-cone stimulus. When adjusted appropriately in phase and amplitude, the L-cone stimulus canceled the perception of flicker, but left the color change unaffected, and thus we could measure the threshold for the color change in the absence of flicker even at low frequencies. In one subject, who was insensitive to S-cone flicker, no canceling L-cone flicker was needed, and we measured the entire function by means of simple forced-choice procedure. Our results show that the temporal-frequency response of the early S-cone pathway is not only shallower than the conventional S-cone frequency response, but it is also shallower than the frequency response implied by suction-electrode recordings of the change in membrane current of isolated S-cone outer segments in response to a brief flash [Schnapf et al, 1990 *Journal of Physiology (London)* 427]. If suction-electrode recordings do accurately represent the response of S-cone photoreceptors, then the S-cone signal must undergo some form of high-pass filtering before the nonlinearity.

◆ **Multistage model for color constancy**

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Two explanations have been proposed for color constancy under illuminant change—adaptation and simultaneous contrast. Although they yield quite similar results, there has been no attempt to integrate them. We will explain contributions of these mechanisms to color constancy by means of a new schematic model. We carried out asymmetric color-matching experiments between test color chips and CRT-generated stimuli, under no-adaptation or full-adaptation conditions under different illuminants. In the no-adaptation condition, the observer matched two stimuli with the right eye only, by viewing the differently illuminated scenes alternately. In the full-adaptation condition, the observer matched two stimuli haploscopically, after 15 min of adaptation to either illuminant. There were two criteria—surface-color match and apparent-color match. We asked the observer to match two stimuli if they appeared to be the same object surfaces for the surface-color match and to match hue, saturation, and luminance for the apparent-color match. The surface-color match showed almost perfect color constancy under both of the adaptation conditions. For the apparent-color match, the results under the full-adaptation condition showed almost perfect color constancy, while there remained a deviation from constancy under the no-adaptation condition. We propose a three-stage model to explain our results. The first stage stands for a mechanism with response regulation, such as adaptation. The second stage has weak spatial-integration ability, such as chromatic induction. The third stage, with complete spatial integration, generates invariant surface descriptions. This model can explain not only the difference in the results between adaptation conditions, but also the difference in the degree of color constancy caused by mode of color appearance.

◆ **Human sensitivity to sinusoidal spectral power distributions: empirical measurements**

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Following Barlow's suggestion (1982 *Vision Research* **22** 635) that colour vision should be analysed by comb-filtered spectra (ie a stimulus whose energy varies sinusoidally with wavelength), the first attempt of this sort was made with square spectral power distributions (SPDs) (Bonnardel and Varela, 1991 *Proceedings of the Royal Society of London, Series B* **245** 165). We have now measured the sensitivity of the chromatic system to sinusoidal SPDs for a large gamut of frequencies (0.4 to 4 cycles per 300 nm) combined with the full range of phases (from 0° to 330°), allowing us to determine the spectral contrast-sensitivity function. To generate SPDs a liquid-crystal display (LCD) is used. The LCD displays computer-generated images and acts as an electronic mask which directly modulates the spectrum formed by an interference wedge. The software produces a mask of any frequency, phase, and contrast. In a three-alternative temporal forced choice, the observer is asked to indicate which stimulus differs from the other two. One stimulus is the reference (unmodulated spectrum, $C = 0$) and one stimulus is the test (modulated spectrum, $C \neq 0$). The reference appears twice and the test once in the three temporal windows (1 s each) in a random fashion. The threshold contrast difference between the test and the reference is determined by an adaptive-staircase procedure. The reciprocal of the contrast needed to distinguish the modulated from the unmodulated spectrum is plotted as a function of comb frequency. The upper envelope of the contrast-sensitivity functions obtained for the different phases is chosen to describe the performance of the chromatic system. This curve, which estimates the transfer characteristics of the chromatic system, shows that it acts as a pass-band filter. From these results, a full discrimination ellipse is also derived and compared with classical discrimination data.

◆ **Colour recognition and simulated illuminant changes**

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Data obtained from two-alternative forced-choice colour-recognition experiments and their relevance to the issue of colour constancy are discussed. A target colour was briefly presented on a CRT monitor in a chromatically diverse surround. After a fixed interval the colour that resembled the target most closely had to be chosen from two alternatives, one of which was in fact the target, that were both spatially and temporally separated. Alternatives differed either in hue, in saturation, or in brightness from the target colour. The uncertainty, as expressed by the error rate, is used as a measure for recognition. Because the displays containing the target and alternative colours are temporally separated and a response is demanded immediately, colour judgments are based on a comparison of the alternative colours with the memorized target colour rather than the target itself. Performances around chance level point to a failure to recognize the alternative as being different from the memorized target colour. A number of experimental manipulations were carried out, ie varying presentation times, contrast environment, and adaptation conditions. In the last case, the colour display was treated as if it was a collection of Munsell papers illuminated by a known light source. By changing the (simulated) illuminant conditions after the target was presented, the alternative had to be chosen in a surround of different average chromaticity. A relatively high tolerance for differences in the (simulated) illuminant invariant component of the target colour was found. As a result, colour recognition is hardly influenced by illuminant changes.

◆ **Studies on colour constancy in goldfish**

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The colour vision system of the goldfish is comparable to that of humans, but goldfish are tetrachromats: they have a fourth, ultraviolet-sensitive cone, which participates in colour vision. Goldfish have to rely on colour as one cue for finding food and recognising conspecifics despite the changing colour of daylight. Therefore we assume that goldfish, as well as other animals with good colour vision, are colour constant. Ingle (1984 *Science* **227** 651) investigated colour constancy in goldfish qualitatively with a two-choice training method, which led to ambiguous results. In our quantitative study we examined the properties of colour constancy by training goldfish at one out of fifteen test fields with hues from blue over grey to yellow. We presented the test fields on a grey background to the goldfish and trained them to choose a bluish grey test field by feeding them in front of it. In the training situation test fields and background were illuminated by white light. In the test situation they were illuminated by yellow light. Without colour-constant vision the goldfish would not recognise the training field in this situation.

But one of the more-blue test fields could resemble the training field under white illumination and the goldfish should choose this one. With colour constancy the fish would not be influenced by the colour of the illumination and would still choose its training field. The test results show that the goldfish still chooses its training field as often as under white illumination. We calculated the relative excitation of the goldfish cones by the various test fields under white and yellow illumination. Blue test field B5 under yellow illumination excites the goldfish cones like the training field under white illumination. Thus, the goldfish had the opportunity to choose a 'physically' identical test field, but they decided in terms of colour constancy.

◆ **Colour appearance: effects of illuminant changes under different surface collections**
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I report the results of a set of experiments designed to study whether the adjustments of the visual system to illuminant changes vary with the surface collection in a scene. Simulations of flat matte surfaces rendered under diffuse illumination were presented on a CRT monitor. Under several surface collections subjects set asymmetric colour matches between a standard object and a test object that were rendered under illuminants with different spectral power distributions. The data from three subjects span twenty-eight different illuminant \times surface-collection conditions. Five different standard objects were used. Two results stand out. First, a change in surface collection did not induce a substantial change in the effect of illuminant changes on the subjects' settings. In this sense, the results are consistent with the hypothesis that the adjustments of the visual system to illuminant changes do not depend on the surface collection. Second, the illuminant-induced changes in the subjects' settings for a given surface collection were well approximated by a von Kries model where the change in the von Kries coefficients is a linear function of the illuminant change. In addition, I tested the hypothesis that the gain of the signal from each cone class is regulated by the photopigment absorptions originating entirely within that cone class. I found some clear deviations from this hypothesis indicating major interactions between the cone classes. A first-order quantification of these interactions is provided.

◆ **Object colour constancy disrupted by changes in colour context**
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The ability to predict changes in the colour appearance of an object under changes in illumination is central to human colour constancy. This ability has been demonstrated for single surfaces in constant-colour contexts (Arend and Reeves, 1986 *Journal of the Optical Society of America A* 3 1743-1751). If the ability is supported by space-average estimates of illuminant colour then it should be unimpaired by changes of context that leave the diversity of reflecting surfaces unaltered. Conversely it should be impaired if, like 'operational' colour constancy (Craven and Foster, 1992 *Vision Research* 32 1359-1366), it is supported by estimates of the constancy of colour relations between the surface and its surrounding context. The question addressed here is whether or not this ability is robust under changes in context. Subjects viewed with one eye a reference surface and surround under a reference white illuminant, and with the other eye a test surface and surround under one of eight test illuminants. The subjects' task was to set the colour of the test patch to the colour that the reference patch would appear under the test illuminant. Reference and test surrounds were two identical samples of forty-eight surfaces in (1) identical random configurations or (2) different random configurations. Performance in condition 2 was significantly poorer than in condition 1. Colour constancy for an object is in this sense impaired when changes in context disrupt local colour relationships.

◆ **Colour constancy with shadows**
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Under different illuminants the same surface reflects different spectra of light; however, despite this, we see the approximately same colour. This is the phenomenon of colour constancy. Many explanations have been put forward to account for this phenomenon. In each, assumptions are made or constraints placed on the world—there is a white reflectance in each scene, there is specular reflection, there is no specular reflection, and so on. A departure from these requirements, and colour constancy is no longer explained. We consider how shadows affect colour constancy. In particular, when a shadow boundary is crossed a single reflectance is seen under two illuminants: the direct illuminant plus ambient (eg sun and sky) and ambient only (sky). The fact that two illuminants are involved provides additional information about the colour of the

surface, even though the spectra of both illuminants are unknown. As follows from the work of Maloney and Wandell, 1986 *Journal of the Optical Society of America A* 3 29–33) we show that, if illuminants and reflectances are described well by two-dimensional and three-dimensional linear models, it is possible to solve for colour constancy at a shadow edge. If the linear model only approximates real cone responses then the attainable colour constancy is dependent on the magnitude of the chromaticity shift between directly illuminated and shadowed cone response vectors—the greater the chromaticity shift the better the colour constancy. Although there are other theories of colour constancy in which multiple illuminants are assumed, ours is unique in that it works with a single reflectance (the most plausible circumstance), as opposed to two (Tsukada and Ohta, 1990, in *Proceedings of the Third International Conference on Computer Vision*, IEEE Computer Society) or three (D'Zmura and Iverson, 1993 *Journal of the Optical Society of America A* 10 2148–2165) reflectances. We carried out simulation experiments to evaluate our method. In line with our theoretical arguments, the degree of colour constancy attained is directly linked to the chromaticity shift between direct and shadow illuminants. Good colour constancy is possible with fairly small colour shifts.

◆ **The interaction of colour and motion in figure-ground segregation**

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We studied how motion and colour interact in figure-ground segregation by determining whether noise in one cue interferes with the segmentation signal carried by the other (cue interference) and whether segmentation is enhanced when the two cues concur (cue concurrence). Observers viewed an array 6.5 deg square of 1000 randomly positioned dots in which the target was a vertical band of dots appearing to the left or right of midline and distinguished from the background dots by a different distribution either of speeds, of colours, or of both. The stimulus design ensures that the task cannot be performed by local-motion or colour-contrast detection. The stimulus was displayed for 100 ms, and was followed after 150 ms by a 1 s mask of moving dots with random speeds and colours. In the motion-isolation case, target and background dots had the same uniform colour, with nonzero luminance contrast. The speed distributions of the background, and target dots were each Gaussian, with different means and standard deviations. Thresholds for correctly locating the target were measured as a function of the difference in target and background distributions. In the colour-isolation case, the target and background dots were held static, while their chromaticities were drawn from different Gaussian distributions. Thresholds were similarly determined as a function of the colour-segmentation signal. In the cue-interference case, motion noise was added to the colour signal (or vice versa) by assigning target and background dots speeds (or colours) drawn from the same nonuniform distribution. We found that thresholds for segmentation by motion were significantly increased by colour noise (for example, by roughly 10% for a colour-noise distribution of 50% red, 50% green). Thresholds for segmentation by colour were likewise increased by motion noise. In the cue-concurrence case, when subthreshold segmentation signals for colour and motion were combined, performance was boosted above threshold, beyond that predicted by probability summation. The results suggest that colour and motion signals interact at early stages, before a global segmentation based on either is decided.

◆ **Colourfulness of colour images of natural scenes: multidimensional scaling**

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It was found that the perceptual quality of the images of natural scenes depended upon their subjective colourfulness when the images were transformed by varying of chroma (Fedorovskaya et al, 1993 *Proceedings of the 1st IS&T/SID Colour Imaging Conference* 37–41). The transformations were done over the colour-point distributions in the CIELUV colour space, where each colour point represented one pixel of a corresponding image. On the basis of the unidimensional scaling of colourfulness it has been demonstrated that colourfulness can be represented as a linear combination of average chroma and variability of chroma. However, such a representation held only within each scene; there was no regular rule to compare different scenes even with significantly different average chroma of the original images. Multidimensional scaling of the colourfulness reveals the relations of different scenes regarding this perceptual attribute. It highlights several factors influencing subjective impression of colourfulness. These factors can possibly be interpreted as a combination of average chroma and variability of chroma, an overall lightness, and representation of hues. The data obtained are compared with those of cluster analysis performed over colour-point distributions in CIELUV colour space.

◆ **The McCollough effect across the menstrual cycle**

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We report a significant increase in McCollough effect (ME) strength experienced by women in the premenstrual phase of the cycle. This investigation was prompted by our failure to repeat with female subjects our earlier observation, with male subjects, of a significantly stronger ME in extraverts compared with introverts (Logue and Byth, 1993 *British Journal of Psychology* **84** 67–84). The data reported here suggest that our failure to repeat our earlier finding of extraversion differences may have been due to variations in ME strength experienced by women throughout the menstrual cycle as a result of ovarian-hormone-mediated changes in cholinergic activity. The ME was induced in fifteen regularly menstruating women at each of the five stages of the cycle. Testing was counterbalanced for all subjects to avoid possible order effects. Colour memory, colour thresholds, response bias, figural-aftereffect magnitude, and critical flicker-fusion thresholds were also measured. Subjects experienced progressively stronger effects throughout the cycle, culminating in a premenstrual peak; this trend was highly significant ($p < 0.001$). A control group of seven oral-contraceptive users showed no significant effect. No significant cyclical variations were observed in the control measures. This suggests that the ME is sensitive to hormonally mediated variations in central cholinergic activity. This interpretation is supported by the sensitivity of ME strength to cholinergic agonists (physostigmine) and antagonists (hyoscine) which decrease and increase ME strength relative to placebo (Byth et al, 1992 *Psychopharmacology* **106** 75–84). The study highlights the difficulties inherent in extrapolating results from studies with males to the female population, where vision may be susceptible to hormonal effects.

◆ **Dependence of Fechner–Benham colours upon luminance adaptation**

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Colour changes in Fechner–Benham subjective colours have been observed at scotopic, mesopic, and photopic luminance levels [Kozac et al, 1989 *Seeing Contour and Colour* (Oxford: Pergamon Press); Campenhausen et al, 1992 *Vision Research* **32** 913–923]. In order to separate mechanisms that possibly interact in producing colours, the temporal dynamics of the subjective colours has been examined. The stimulus was an arc (12 min radial width, 45 deg angular extent) of a rotating (7 cycles s^{-1}) Benham disc. The angular position of the start point of the black arc with respect to the onset of the white background determined the start phase of the arc. The disc was presented for various durations (1, 2, 4, 8, and 16 rotation cycles). Steady (22 cd m^{-2}) and transient (dark to 22 cd m^{-2} luminance) adaptations were studied. Responses of four subjects (two naive ones plus the two authors) were collected with a hue-naming procedure. Changes in colour names, rather than colour names per se, were analysed. For every observer, the smaller the start phase of the arc, the greater the change of colour associated with a change of exposure duration. This effect was most observable with transient adaptation. For instance, with transient adaptation, the colour of arc number 1 (start phase 0°) changed from reddish to purple and bluish as the presentation time increased from 1–2 cycles (143–286 ms) to 8–16 cycles (1143–2286 ms). On arc number 7 (start phase 135°), the blue colour changed only slightly with presentation time for either adaptation condition. Moreover, under steady adaptation, the four unique hues were equally balanced for every presentation time when the start phase was around or slightly smaller than 90° , whereas, with transient adaptation, the four unique hues did not cancel out so dramatically and a residual greenish colour was perceived for every presentation time when the start phase was slightly greater than 90° . It seems that Fechner–Benham subjective colours could emerge from the competition between time-dependent and adaptation-dependent mechanisms.

◆ **Dominance of the color green in apparent transparency**

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Kanizsa [1979 *Organization in Vision: Essays on Gestalt Perception* (New York: Praeger)] has revealed several fundamental rules of shape and reflectance governing the phenomenon of the overlapped section of two partially overlapping figures being perceived as transparent; however, a chromatic effect has not been clearly shown. Oyama and Nakahara (1960 *Japanese Journal of Psychology* **31** 35–48) did examine the effect, by using color chips and a rotating disk, and showed that the overlapped section of figures on a gray background consistently appeared to be of the advancing hue. However, we find differently, with the color green emerging as a dominant color regardless of what color it is paired with.

We tested a maximum of seven luminescent colors in a total of three experiments in a dark room by means of a CRT display. Each luminance was kept constant. Dominance was determined by testing how far ambiguity occurred from the equal-quantity mixture point of the two colors. We first tested with a cross-shaped figure, and found that green overcame all other colors, without anisotropy of visual space. Second, we used a pair of rectangles with separation between them to test for the advancing effect on the CRT screen. We found that the advancing order was not $R > Y > G > B$, as Oyama and Nakahara had found, but $R > G > Y > B$, with a difference between transparency and the effect. Finally, we added a depth cue by taking a figure of two partially overlapping squares in three colors—two out of red, green, and white, and one mixture color—and changing the sizes of each of the squares while keeping the size of the overlapped section constant. We found that the color green was dominant, and it ruled out depth effect. These results should be further interpreted by analyzing differences of color appearance, viewing condition and surrounding lightness, and L/B ratio.

◆ **Temporal asymmetry during a colour-discrimination task**

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A colour-discrimination task, using a matching-to-sample paradigm, exhibits a pronounced asymmetry of detectability (d'), depending on which stimulus is the sample and which the test. We used two stimuli (1, 2) to form four types of trials, (11, 12, 22, 21), thus this specific paradigm enables us to calculate d' for each of the two pairs separately (11, 12 and 22, 21). The stimuli were two adjacent equiluminant colours, which were squares (or circles, in some experiments) of 0.3–3.2 deg, and were presented at the fixation location. Separate calculation of d' for each one of the two pairs shows a significant difference between them. The distance in the colour domain between the two stimuli is the same in both pairs. We can therefore conclude that the difference in d' is due to the order of stimulus presentation. We have found that the direction of the asymmetry, in the colour domain, is consistent neither across the subjects nor across different colours for the same subject. To avoid the possibility that the subjects pay more attention to one of the pairs, in an additional experiment we separated the two pairs into different blocks. The results show the same trend of asymmetry, indicating that this asymmetry is not determined by a process of attention. In an additional experiment, we found that this asymmetry phenomenon is not local, within the range of 0.3 deg. The asymmetry was preserved when we presented the two successive stimuli 0.3 deg apart. We discuss two possible explanations for this temporal asymmetry—adaptation and short-term memory. To distinguish between these two explanations, we studied the influence of the time interval between the two colours on the magnitude of the asymmetry effect.

◆ **Colour constancy in nongrey average surrounds: influence of luminance and simultaneous contrast**

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In several colour-constancy algorithms it is assumed that the average chromaticity of a scene determines apparent colour. This assumption was tested in a previous experiment employing two Mondrians with equal average chromaticity (Fuchs, 1991 *Perception* 20 Supplement, 100). One of the Mondrians had grey average reflectance and bluish illumination (the changed-illumination condition), the other one white illumination and a nongrey average reflectance due to a large area of a single blue reflectance (the blue condition). The Mondrians were simulated on a colour monitor. Subjects matched the colour appearance of a test field from memory with one previously learned in a white-illumination/grey-average-reflectance Mondrian. Despite having equal average chromaticity, the two conditions led to different results. The present experiment is an investigation of whether the fact that in the blue condition the luminance of the blue reflectance was lower than the luminance of the other chromaticities led to the observed difference. Also, the influence of the dark background that separated the coloured fields was investigated. The previous experiment was repeated with a Mondrian with directly adjacent colour fields. Two versions of the blue condition were tested, one in which the luminance of the blue reflectance was 25% lower than the mean luminance, and one in which it was equal. Matches in the changed-illumination condition were not altered by removing the dark background. Results for the blue condition, however, became more similar to those for the changed-illumination condition. Increasing the luminance of the blue reflectance reduced the differences between the blue condition and the changed-illumination condition further but did not eliminate them. This confirms that not only average chromaticity but also the set of chromaticities of which a Mondrian is composed influences colour appearance. How large its influence is seems to depend on several, as yet largely-unknown factors.

◆ **A model of the human visual system: colour perception of aperture colours and the effects of chromatic adaptation**

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Psychophysical data on perception of aperture colours are used as a guide for development of colour analysis by a model of the human visual system. Channels carrying information about colour are represented by summed responses of midget C-type and L-type cells. Spectral energy distribution of any coloured stimulus produces within the cell types a unique pattern of activities from which amounts of each of the hues (ie red, green, blue, and yellow), whiteness, brightness, and saturation can be determined. The present analysis is restricted to the blue-cone region of the parafovea. For aberration-free dispersion and no chromatic adaptation, the psychophysical and model data are in good agreement as to the three attributes of aperture colours—hue, brightness, and saturation. Owing to univariance, information about spectral distribution of the stimulus cannot be used, which creates a problem as how to normalise coloured stimuli to a common set of standards. Normalisation of the outputs of the retinal cells to a common white is used. Two forms of adaptation are added to the model. ‘Self-adaptation’ is produced by the coloured stimulus itself. The second form of adaptation is due to an external chromatic light source. Self-adaptation is the basis for the Bezold–Brücke hue shift. Adaptation due to an external light source produces cone densitisation by altering their gains. These changes are proportional to the quanta catch for each cone type, which is dependent on the sensitivity of the cone type and spectral distribution of the coloured stimulus. However, changes in hues are modified by colour opponency pairing red with green and blue with yellow. Brightness is increased and saturation is decreased as self-adaptation is increased. For an external light source, the opposite occurs. However, effects of an external adaptation on the attributes of aperture colours are modified by self-adaptation.

◆ **Precise location assessment under isoluminance**

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In our previous study (Petrauskas et al, 1993 *Perception* 22 55) we showed that the human visual system is capable of detecting small offsets of isoluminant vernier targets within hyperacuity limits. To investigate spatial mechanisms underlying precise location assessment under isoluminance, vernier acuity was studied by means of two kinds of stimulus—red targets on a green background and yellow targets on a blue background. The thresholds were assessed for upper and lower targets of both the same and different chromaticity. We found no significant difference in thresholds in all the above cases for the three normal subjects. The results suggest that detection and spatial processing take place independently along the three known directions of colour space, the outputs of which then are analysed at higher levels of the visual system to allow judgment of the relative position of elements of the scene to be obtained with hyperacuity precision. A distributed-representation approach which incorporated chromaticity-sensitive double-opponent neurons with both even and odd-symmetric receptive fields is used to account for precise location assessment within each direction of colour space.

◆ **Successive visual analysis and McCollough-type achromatic aftereffects**

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McCollough-type aftereffects are produced not only in response to the presentation of gratings, but also after simultaneous presentation of any two stimuli that differ from each other by two strictly fixed characteristics—orientation and brightness, or contrast and shape, or brightness and contrast, etc. ‘Achromatic’ aftereffects have an interesting peculiarity: after adaptation to a black–white vertical grating of high brightness and a black–white horizontal grating of low brightness 80% of the observers see on the combined grating the vertical ones to be bright (‘positive’ effect) and 20% the horizontal ones (‘negative’ effect). Since the ‘positive’ McCollough colour effects never occur, this effect needs a special explanation. The same subjects were asked to group cards of different colours hatched with gratings of different orientation and brightness. The subjects were to lay out the cards according to any particular characteristic. 90% of the subjects who had acquired a ‘positive’ achromatic effect gave preference to orientation, 85% of those who had acquired a ‘negative’ effect showed preference for brightness. A new series of experiments was carried out to determine whether this preference was dependent upon any other factors or not. The experimental findings showed that if the subjects were asked to group several objects into two classes according to their shape, colour, brightness, and orientation without giving the matter any consideration they gave primary preference to the

shape, then to the colour, orientation, and brightness. But if the subjects were asked to group them after consideration, they gave equal priority to the shape and colour over the other two. The orientation was always analysed first, then the brightness, but always after the shape and colour. The mechanisms of colour and brightness constancy, and cortical detectors as well as successive visual-analysis processes must be involved in the induction of the McCollough effect.

◆ **A new class of red-green colour-vision deficiency**

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Nagel's anomaloscope (Nagel, 1907 *Zeitschrift für Augenheilkunde* **17** 201–208) has long been recognised as the clinical instrument for the definitive differential diagnosis of congenital red-green colour-vision deficiencies. This instrument presents spectral lights in two juxtaposed fields, one yellow (Y) and the other a mixture of red (R) and green (G). Colour matches are made by adjusting the ratio of R to G and the radiance of Y. Subjects who accept all mixtures, including both pure R and pure G, as colour matches ($R = Y$ and $G = Y$) are classified as dichromats. However, Nagel's anomaloscope (designed on the direct-vision-spectroscope principle) cannot present the twofold wider colour gamut of the comparison $R = G$. Consequently, it may be that some 'Nagel' dichromats are actually anomalous trichromats with extremely poor hue discrimination. In several large population studies, often cited in the literature, Nagel's anomaloscope was used to determine the relative frequencies of the various red-green deficiencies. It is possible, therefore, that the incidence of true dichromacy has been overestimated. This issue is being addressed by utilising a research anomaloscope to present the three comparisons, $R = Y$, $G = Y$, and $R = G$, in a standard 2 deg field. To date we have found, in a group of nine 'Nagel' dichromats, two deuterans who reject $R = G$. These, by extension of the terminology describing anomalous trichromats as simple or extreme, must be very extreme. Since simple and extreme anomalies are distinct at the molecular-genetic level, it would be reasonable to suppose that a very extreme variety is, too. Consequently, the loss of colour discrimination approaching but not at the dichromatic level, in these two very extreme deuteranomalous trichromats, may be a manifestation of an anomalous 'middle-wave' photopigment which is spectrally very close to the normal long-wave pigment.

◆ **A comparison of brightness matching and flicker photometry over the full mesopic range**

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As part of a collaborative programme with Laboratoire de Physique Appliquée, Muséum National d'Histoire Naturelle, Paris, visual matches were made by twenty observers, from 0.03 td to 100 td on a central 10 deg field by means both of heterochromatic flicker photometry and of direct-comparison techniques. Results were obtained at nine wavelengths between 445 nm and 630 nm and at nine illuminance levels by using four channels of a six-beamed Maxwellian-view instrument. Plots of relative sensitivity versus illuminance at each wavelength were compared for the two methods. The direct-comparison brightness matches showed a smooth transition of sensitivity with illuminance. However, the flicker method exhibited a step change at approximately 1 td. Spectral-sensitivity curves for both methods at the nine illuminance levels have been calculated and compared with the $V(\lambda)$ and $V'(\lambda)$ curves.

◆ **Identifying color mechanisms from chromatic-discrimination data by analysis of residuals**

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Poirson et al (1990 *Journal of the Optical Society of America A* **7** 783–789) advance the hypothesis that color-discrimination measurements contain insufficient information to permit estimation of the linear chromatic mechanisms responsible for discrimination performance. They could not reject this indeterminacy hypothesis in experiments in which 2 deg disks with a Gaussian time-course were used. Cole et al (1993 *Journal of the Optical Society of America A* **10** 38–51) using 2 deg spatially blurred test lights flashed for 200 ms, conclude that chromatic-discrimination-performance data can be used to estimate the spectral sensitivities of chromatic mechanisms in color space. Comparison of the two sets of results is complicated by three factors. First, the stimuli used differ in spatial and temporal characteristics. Second, the models of chromatic discrimination used in fitting data differ in the two papers. Third, the experimental methods and analyses employed by Poirson and colleagues are not, in fact, sufficient to demonstrate that chromatic mechanisms are indeterminate. We derive necessary and sufficient conditions that

chromatic-discrimination data provide no information concerning underlying chromatic mechanisms. We report experimental tests of these conditions for 1 deg disks, modulated at 1.5 Hz or at 12.5 Hz. These tests include analyses of the residuals of fits to both models. We do not reject the indeterminacy hypothesis.

APPLIED PSYCHOPHYSICS

◆ The perception of geometrical features on a hexagonal grid

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The geometrical features characterising object shape, size, and orientation are the clue for correct and accurate decisionmaking in object-recognition and image-understanding tasks. Image-digitisation procedures insert distortion into object size, shape, and orientation and make their visual perception difficult. The computer processing of digital images makes this problem more severe since these distortions affect crucially the computation of the corresponding geometrical features. To make the perception of the digitised images comparable to the natural perception mechanisms being performed by the eyes of human beings and animals, hexagonal grids were introduced (Mersereau, 1979 *Proceedings IEEE* 67 930–949). The main advantages of these grids as compared with rectangular ones are the absence of the problem of four or eight neighbours—every hexagonal pixel (hexon) has six equidistant neighbours; and that a hexagonal grid provides more fine-angle resolution. That is why hexagonal grids give us a more accurate discrete representation of an object border and therefore its size and shape. We compare the measurements of geometrical features when rectangular and hexagonal grids are involved. The features under consideration are area, perimeter, thickness, compactness, etc. We simulate the rectangular and hexagonal grids by special averaging procedures in which fine-resolution images are used as input. The relationships of accuracy of geometrical-features estimation with object size and orientation are shown. It is established that the representations on the hexagonal grids provide the lowest variance of geometric-feature estimates for objects with different orientation. Hexagonal grids give more-favourable conditions for correct object-recognition performance.

◆ A computational retinex algorithm

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Colour constancy in the human visual system is a complex process involving the retina, the lateral geniculate nucleus, and the visual cortex. From the viewpoint of the retinex theory, we have developed an algorithm by which the colours present in the different regions of a visual scene are coded in such a way that, under certain conditions, they become invariant to changes in the illuminant. From an image in a CCD colour camera, the RGB images are digitised in a grey scale from 0 to 255. For each of these images, a series of relations between the luminosities or grey levels of every colour in the scene are established. We have observed that, when the illuminant is changed, for instance from daylight to a reddish light, the relative positions of the luminosities of the colours are approximately invariant. From these observations, in each RGB channel, we can obtain a set of three descriptors for any colour in the scene. The recognition of any colour is carried out by means of the colorimetric information of the rest of the colours present in the scene. By means of Mondrian patterns (with Munsell chips) we have shown that these descriptors remain approximately constant under different illuminants. This new chromatic codification can be utilised for creating an algorithm formed by a process of recovery, based on a colour database (Munsell chips) coded by these new descriptors. These results may help the development of artificial vision systems based on colour detection and recognition, which have to work under changing illumination. On the other hand, it may also help us to understand the colour-coding process of the human visual system.

◆ A modular, portable model of image fidelity

A B Watson, A J Ahumada, Jr (NASA Ames Research Center, Moffett Field, CA 94035-1000, USA)

There is a persistent need for a trustworthy model of perceptual-image fidelity, especially in applications such as image compression and display design. A fidelity model provides a measure of the visual discriminability of two images. Ahumada [1993 *Society for Information Display International Symposium Digest of Technical Papers* Ed. J Morreale (Playa del Rey, CA: Society for Information Display)] has previously shown that the existing fidelity models may be

categorized according to their inclusion of various canonical properties, such as a contrast-sensitivity function, or spatial-frequency channels. This suggests that research would be aided by the availability of a modular model, in which these components could be easily inserted or removed. A further impediment to research in this area has been that most models are written in low-level languages and are consequently large, nonportable, and difficult to understand, modify, and maintain. We therefore believe research would also be aided by models written in high-level languages. To serve both of these purposes, and to honor our conference host for his lifetime dedication to the problem of image quality, we offer a modular model written in the high-level language, Mathematica. We demonstrate this model and show how it may be modified.

◆ **Image quality and contrast of CRTs**

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5600 MB Eindhoven, The Netherlands)

In the whole history of CRT television it has been realised that contrast is one of the most important determinants of image quality. As a consequence of recently developed techniques of advanced digital signal processing and of better control of imaging within the tube, the question how contrast and quality are related has become even more urgent in the last few years. In our view, the issue of contrast is strongly related to the specific features of the transducer CRT and its physical behaviour. Therefore, we present a simple but sufficiently accurate model of achromatic-light production in a CRT. This will clearly point to the problem of the definition of contrast in general. Subsequently, we will present the results of two experiments, in each of which the effect of the most prominent parameters of the imaging chain on image quality and perceived contrast is investigated. From these experiments it will appear that it is very difficult to isolate the effect of brightness contrast on image quality. The reason is that most changes in an image or in the settings of a television set will also have their effects on colour and sharpness, whereas the environmental conditions enter in a nonlinear way too. These results can be compared with the theoretical results of a brightness model. Within the model we apply, the quite general need for a higher-contrast parameter, gamma, can be attributed to the available working range of the contrast-detection mechanism and its sensitivity at different working levels. In fact, this is equivalent to keeping the dynamic range of the perceived brightness-contrast constant. The most important physical parameter in this respect is the quotient of the maximum and minimum luminance level in the reproduced image.

ATTENTION, VISUAL SEARCH, AND EYE MOVEMENTS

◆ **Absence of threshold elevation at isoluminance for displacement during saccades**

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It is well known that the displacement threshold is elevated when it occurs during a saccadic eye movement. One of the possible interpretations of this phenomenon is saccadic suppression of motion perception. Since displacements produce motion sensation, displacements during the fixation period are likely to be detected by motion detectors. In this case, the displacement threshold should be elevated for isoluminant color stimuli, since the motion signal is weak for isoluminant stimuli. If there is saccadic suppression of motion perception, the elevation of threshold may not be seen for the displacement during saccades. In order to examine this issue, we investigated the effect of luminance contrast of red/green color gratings on the displacement threshold at fixation and during saccades. Horizontal red/green color gratings were used as stimuli. The luminance contrast of the grating varied between -20% and 20%, including 0%. The detection threshold of the displacement was obtained by the method of constant stimuli. The observer made a saccade to follow a fixation point that was displaced horizontally by 5 deg. The grating was displaced vertically by a randomly selected amount either during the saccade (saccade condition) or 300 ms after the saccade (fixation condition). The observers responded as to whether or not they could detect the displacement. The displacement size that gave 50% correct responses was defined as the detection threshold. The results show that the threshold increases as luminance contrast of the grating decreases in the fixation condition, whereas it is approximately constant and independent of luminance contrast in the saccade condition. These results suggest that the displacement during the fixation period was detected on the basis of motion signal, while that during a saccade was detected on the basis of different cues. The motion-sensitive mechanism does not seem to work for the displacement during saccades.

◆ **Do women think faster than men?**

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Investigating brain potentials associated with a memory-scanning task (Sternberg paradigm), we found shorter reaction times and higher frequencies of brain waves in women than in men. Observers had to memorise a single letter presented for 1 min on a monitor screen in one condition, and seven letters presented simultaneously in the other condition. Then, in seventy trials, single letters appeared for 1 s on the screen, and observers decided whether or not the letter was part of the (one-item or seven-item) list they had memorised. Observers indicated their decision by pressing a push-button. The computer program producing the stimuli also recorded the responses and calculated percentages of correct responses as well as reaction times. Simultaneously, we recorded electrical brain activity with four electrodes over the occipital brain in all thirteen observers. After the experiment, each sweep was Fourier-transformed and the power spectra were averaged for the seventy sweeps of each condition. Reaction times for the seven-letter condition were longer than those for the single-letter condition, on average, by 169 ms (standard error ± 25.0 ms) in women and by 191 ms (standard error ± 18.5 ms) in men. This indicates a processing time of 28.2 versus 31.8 ms item⁻¹ for women and men, respectively. The power spectrum in the corresponding frequency bands of 35 Hz (women) and 29 Hz (men) was significantly more pronounced in the seven-letter than in the single-letter condition, while the results of women, when analysed by using the 'male' frequency band, or vice versa, showed no significant difference between the two conditions. The gender difference was significant on the $p = 0.0033$ level for the frequency band around 35 Hz and $p = 0.0001$ for the frequency band around 29 Hz (unpaired, two-tail t -test). The results indicate that periodic changes of brain potentials occur during memory scanning that might reflect the sequential processing of individual items. This corresponds well with the processing differences between parallel and serial visual tasks we found earlier (Albrecht et al, *Investigative Ophthalmology*, in press). Moreover, women might have a higher frequency of processing than men for this kind of task.

◆ **Letter migration in RSVP tasks**

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We investigated temporal letter migrations in rapid-serial-visual-presentation (RSVP) tasks in which Japanese Kanji words and pseudowords were used. We found that migration occurred more often with distractors preceding targets than with distractors following targets with visually complex words. Two-Kanji-character words were presented in RSVP. Each trial consisted of eleven fillers and a target embedded near the middle of a stimulus sequence. Fillers were presented in cyan and the target was defined as a white item. Subjects were required to report the white items. Each word was presented for 35 ms, with 90 ms ISIs. The fillers preceding and following the target were defined as distractors. Our experiments involved two conditions. In the word condition, the first characters of the targets and the second characters of the distractors formed new words. The second characters of the targets and the first characters of the distractors also formed new words. That is, the possible recombinations were of the 'line-lace-lane-lice' type, where 'line' was a target and 'lace' was a distractor. A two-letter cluster such as 'li' corresponds to a Kanji character. In the pseudoword condition, recombinations of targets and distractors formed pseudowords. Three main results were obtained. First, temporal letter migration was found when targets and distractors were presented serially in the same position. Second, migration was more frequent for the word condition than for the pseudoword condition. Third, migration with the distractor preceding the target was more frequent than that with the distractor following the target. These results are in line with the findings in RSVP tasks with Kanji characters that are visually complex. It is suggested that letter configurations and colors are processed independently at an early stage in word recognition. Moreover, temporal letter migration suggests that letters in words are processed independently in RSVP situations where attention is overloaded.

◆ **Partial-report cues do not select representations but processing regions**

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In previous studies we presented evidence that the partial-report procedure does not reflect selection from a visual sensory memory (eg Schulz, 1991 *Perception* 20 501-512). Specifically, in 1990 (Schulz, *Perception* 19 404) we devised the partial-visual-search task, demonstrating

that, although partial search is superior to whole search, it shows no decline or a very flat decline over an interval of 1 s which proves to be strongly dependent on the target-noise-similarity relation, independently of cue timing. A possible conclusion is that the cues do not select early representations, but help to construct them by capacity allotment.

We now report a variant of this task in which subjects had also to report the letter adjacent to a just-detected target letter (search-report paradigm). Though partial search was again superior to whole search and the secondary task superior under partial-search-task conditions to performance under whole-search conditions, it showed no decline even in the partial (report) condition. Clearly, this task was more difficult than the search task (corrected for guessing). However, even if it is expected that no decline in a detection/search task will occur because of its low difficulty, the secondary task of reporting the adjacent letter should show a decline caused by persistence, at least in the more difficult partial-search condition. Thus, as there was no persistence effect even in this task, though it was far more difficult than the detection task, we conclude that the cues control the range of activated representations of the display, thus causing the difficulty costs—similarly to visual attention distributions. If this attentional explanation is correct, the pattern of time independence should be unaffected by a variation of stimulus luminance. This experiment is under way now.

◆ Experimental testing of the corrected Listing's Law

A P Petrov (Computer Vision Laboratory, Russian Research Centre 'Kurchatov Institute', 123182 Moscow, Russia)

It was reported (Petrov, 1992 *Proceedings of the 9th Israeli Symposium on Artificial Intelligence and Computer Vision* pp 93–102) that in experiments with afterimages the human visual system was found able to determine gaze direction accurately, including the vertical component of the fixation-point position. A theoretical consideration based on the so-called fusion equation led to the hypothesis that cyclotorsion is used for determination of the elevation angle (as variables in Listing's Law). I discuss this hypothesis and argue for its acceptance after testing of the reformulated Listing's Law referred to here as the corrected Listing's Law (CLL): the difference of torsions of the left and the right eyes is a one-to-one function of the position of the fixation point in the visual field and does not depend on previous movements of the eyes or the subject.

Results are presented of an experimental verification of the CLL. The positions of the subject's eyes were recorded with a camera placed on the axis of the right eye and taking pictures of the left eye through a mirror system in such a way that the pictures of both eyes were taken simultaneously and in paraxial mode. Thus we could measure the torsional angles during head tilting and other nonsymmetrical actions of our subjects (pressure upon a shoulder, etc). The collected data were in agreement with Ferman et al's findings (1987 *Vision Research* 27 929–951 of systematic and random deviations of the torsion of each eye, measured separately, of about 10 deg from Listing's Law but they showed very small errors in following the CLL formulated above. Actually, those errors did not exceed the accuracy of the measurement system we used, ie 30 min arc. It is concluded that the CLL is fulfilled by the human visual system in the situations investigated.

◆ Functional visual fields and attentional capture

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It has been reported that functional visual fields are determined by attentional factors such as an instruction to a spatial location (Engel, 1971 *Vision Research* 11 563–576). The purpose in this study was to investigate the effect of the cue to evoke attentional capture on the functional visual fields. Functional visual fields for the discrimination of the orientation of the T-shaped ('-|' or '|-') target among L-shaped noise were measured under no-color-cue and color-cue conditions. The target was composed of a vertical and a horizontal line segment. The stimulus pattern was presented for 160 ms, and the EOG was monitored to eliminate trials in which eye movement occurred. There were two search conditions—feature search and conjunctive search. In the feature-search condition, because each noise element was composed of two diagonal line segments, the target was defined by the difference of the orientation of line segments. In color-cue conditions, the horizontal bar of the target was colored green. The effective expansion of the functional visual field with color cueing was demonstrated. In the conjunctive-search condition, the target was defined by the conjunction of the two line segments. Without the color cue, the functional visual field was very small. In the color-cue condition, the functional visual field expanded to the same extent as in the feature-search condition with color cue. It is suggested that the feature that effectively captures the observer's attention determines the size

of the functional visual field. If the featural information is available, the functional visual field is restricted. A model related to the modified guided-search model is proposed to account for the results.

◆ **Fixed or flexible information-picking strategies in scene recognition?**

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A puzzle in the recognition of complex images is that a scene composed of many objects can be recognized in a single glance, as quickly as one component object. This suggests that fast scene recognition could bypass the extensive bottom-up approach to recognition in which it is proposed that one identifies a scene after identifying a few component objects. We have shown (Schyns and Oliva *Psychological Science*, in press) that scene recognition is bipolar: the very first stages of processing could use scene-specific information available at coarse spatial scales while the later stages would rely on object-specific fine-scale information. In the current research we investigate whether this scene-before-objects information-picking strategy is fixed in perception, or flexible and dependent on task demands. We used hybrid stimuli—stimuli which associate a different scene with different spatial resolutions of the image. We presented subjects with animated sequences of two hybrid scenes. Each sequence presented simultaneously two possible interpretations to the visual system: a scene-before-object and an object-before-scene interpretation. Since each interpretation was associated with a different scene, by this method we could test whether we could change the scene-before-object strategy observed in Schyns and Oliva (in press). One group of subjects was instructed that objects (the object group) were the most relevant information for scene recognition. The other group (the scene group) was simply instructed to categorize the scene as quickly as possible. We observed a strong scene-before-object bias in the scene group, but scale selection moved in direction of an object-before-scene in the object group. Our results suggest that spatial-scale selection for high-level processing might not be fixed or hard wired in perception, but flexible, or soft wired—that is, rewired by attentional mechanisms.

◆ **Discrimination of gaze direction**

H P Snippe, R J Watt (Department of Psychology, University of Stirling, Stirling FK9 4LA, UK)

We studied discrimination for gaze direction as an example of quantitative psychophysics applied to naturalistic stimuli. The stimuli used are digitised photographs of human faces, displayed on a computer monitor. All faces are fronto-parallel with respect to the camera, but vary in gaze direction. Also, viewing in the experiment was fronto-parallel with respect to the display. Under these circumstances gaze-direction-discrimination thresholds correspond to a rotation of about 3° of the eyeball of the persons photographed. This threshold was independent of viewing distance, ie scale invariant, perhaps surprisingly for this task. At the largest viewing distance for which this scale invariance still applies, the 3° eyeball-rotation threshold corresponds to a visual angle of about 10–15 s arc for the observer in the experiment. Thus, as might be expected, human observers can perform very well in this task. Discrimination thresholds are very robust against a decrease of presentation time, even when pre-stimulus or post-stimulus noise masks are used. Correct fixation for the observer, however, is important; performance rapidly deteriorates in eccentric vision. We are currently investigating the effects on discrimination thresholds of spatial filtering of the images used, and of the addition of spatially filtered external noise.

◆ **Accommodation, convergence, pupil diameter, and eye blinks with a CRT display flickering near critical fusion frequency**

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Subjects observed an array of text on a variable-frequency cathode ray tube (CRT) operated at different refresh rates near the fusion limit. The CRT had a fast phosphor with virtually full temporal modulation up to 100 Hz. The bright (50 cd m⁻²) screen area (12 cm × 17 cm) was presented at a viewing distance of 50 cm. Various visual functions were measured in series of tests of 3 min duration. In experiment 1 subjects viewed with both eyes. At the repetition rate of 50 Hz (which flickered visibly for most subjects), the mean pupil diameter was 0.055 mm smaller than at 300 Hz ($n = 19$, $p < 0.05$). No effect was found in accommodation and fixation disparity, ie the precision of convergence. In experiment 2 vision was monocular so that

convergence-induced accommodation could be ruled out. The 300 Hz-condition was compared with the lowest repetition rate that did not produce visible flicker for each subject. These rates fell within the range 55–90 Hz (mean 70 Hz). At the lower frequency, mean accommodation was 0.06 D weaker ($n = 17$, $p < 0.05$), the median eye-blink duration was 6% shorter ($n = 23$, $p < 0.05$), and the mean eye-blink interval was 15% longer ($n = 23$, $p < 0.05$). Pupil size was insignificant. Some individual data differed strongly from these mean results. Some subjects showed no effects, whereas others had significant effects that were replicated in repeated sessions in single cases. In general, the observed effects were subtle and no direct adverse consequences are to be expected. But—also in view of research on eye movements [eg Kennedy and Murray, 1993 *Nature (London)* 365 213]—it is possible that the susceptibility of visual functions to nonvisible intermittency of light might contribute to visual fatigue in extended periods of CRT use, at least in sensitive individuals.

◆ **Distribution of attention throughout the visual field in traumatic-brain-injury patients**

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There is a little consensus about appropriate evaluation and treatment of attention deficit. In the present study we developed a quantitative approach for studying of attention in traumatic-brain-injured patients who suffered from nonlocalised diffuse brain damage. In normals, allocation of attention, by precuing to the 'luminance centroid' (the point of origin of the object-centred coordinate frame) of a simple visual pattern, improved recognition significantly owing to the extraction of the essential information about the object (Pavlovskaya et al, 1992 *Ophthalmic and Physiological Optics* 12 165–167). Now we have attempted to determine whether brain trauma produces a deficit in the shifting of attention to the luminance centroid of patterns which appear at different locations in the visual field. A pattern-identification task was given to six traumatic-brain-injury patients and to six control subjects under time-pressure conditions. All observers fixated on a central point on a computer screen. Stimulus presentation (five letter-like figures with size of 3 deg) was preceded by a precue signal that appeared at 5 deg of visual angle to the left or right of fixation. For trials that were further considered as 'relevant' ones, the precue and the stimulus appeared in the same hemifield and, moreover, the precue was displayed at a locus that corresponded with the luminance centroid for the given stimulus. For 'irrelevant' trials the target occurred in a different position from the precue but in the same hemifield. On 'cross' trials the target appeared on the side opposite the precue, demanding either a leftward or a rightward shift of attention across the central meridian. We found that normal subjects perform best in the 'relevant' condition (especially in the left hemifield). There was no significant difference in performance on 'cross' trials for normal controls. The patients did not exhibit any difference in performance under 'relevant' in comparison with 'irrelevant' conditions in either hemifield, but on 'cross' trials there was a significant failure in leftward shift of attention from the right hemifield to the left one. We examined one of our patients after 1 year of rehabilitation and found a marked improvement in this aspect. In conclusion, diffuse brain damage may cause impairment in both the ability of patients to extract the essential information about the object by allocation of attention to the LC and the ability to move attention from the right hemifield to the left, demonstrating the different role of the two hemispheres in attention control.

◆ **Visual processing during advanced reading**

VI Belopolskii (Institute of Psychology, Russian Academy of Sciences, Yaroslavskaya 13, 129366 Moscow, Russia)

Most models of skilled reading assume a word-by-word strategy of information acquisition. This corresponds with adults' average reading rate (200–250 words per minute), although a certain proportion of readers read up to twice as fast. Does this mean that during advanced reading the perceptual span increases and/or the fixation durations decrease as compared with in normal reading? To test this hypothesis, parameters of eye movements during comprehended reading were recorded in two advanced and two normal readers. In addition, the presented texts had different spatial layout in terms of line widths (20–120 characters). The normal and advanced readers showed reading rates in the ranges of, respectively, 218–430 (mean 308) and 413–791 (613) words per minute. The number of fixations at 100 words was lower and the mean amplitude of saccades was higher in advanced than in normal readers. Although a clear effect of line width on reading rate was not obtained, all subjects had lengthened their saccades with an increase in line width in a linear fashion. Unexpectedly, both advanced readers showed increases of fixation durations (333–339 ms), which typically had bimodal distributions.

The longer a fixation, the more pronounced was the oculomotor drift that accompanied it. The results allow us to suppose that a perceptual span of 2 or 3 words as well as fast and fluent attentional dynamics are the main features of advanced readers' reading strategy.

◆ **Characteristics of eye macromovements**

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The recording of eye movements was performed with an oculometer. The oculometer consisted of two-dimensional transducers and diamagnetic coils, which were placed on the eyeballs in the limbus cornea area (designers of the device, K Krichchiunas et al). The screen, adjusted for the investigation, had 104 red lights as test objects, which were spread out in circles at distances of 4, 8, 12, 16, and 20 from the centre. Twenty-four persons with binocular vision were investigated.

Analysis of the clinical data showed some consistencies in the turning of the eyes in corresponding directions. In cases with a straight position of the eyes and normal binocular vision, the eye turns to the side and returns to the centre on the special trajectory which is similar in shape to a leaf. The leaves are wide or narrow, depending on the location of the object on the screen. It is supposed that narrow leaf shapes indicate the work of single muscles and wide ones the work of groups of muscles. Observing the path of formation of the leaf shapes, we have found that if the test object was in the diagonal meridian at the inferior lateral part of the upper square, then the eye, on its way to the periphery, had its trajectory bent upwards, and on its way to the centre the trajectory bent downwards. If the red light was in the diagonal at the superior part of the lateral upper square, then the trajectory of the eye bent downwards, and return trajectory was bent upwards. The trajectory of eye movements from the centre and back had a precise direction in the whole field. The peculiar and precise path of eye movements is supposed to depend on the muscles that move the eyes, which work in the appropriate part of the trajectory.

◆ **Prolonged centrifugation decreases ocular torsion**

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Centrifugation for 1 h with a Gx-load of 3g provokes postural instability and motion sickness afterwards for several hours (Bles and de Graaf, 1993 *Journal of Vestibular Research* 3). It was shown that a cardiovascular cause was highly unlikely, which focused our attention on the vestibular system, especially the otoliths. In the present study we investigated the effects of centrifugation on the otolith-induced ocular torsion (OT). OT was measured at tilt angles of 0°, 10°, 20°, 30°, 42°, and 57° to the left and to the right by means of a tilting chair (TNO three-dimensionally-rotating chair). In each position eye movements were recorded on videotape by means of binocular video-oculography for off-line analysis of OT. These measurements were performed twice, once before and once after a 1 h centrifuge run. The centrifuge (located at the Netherlands Aerospace Medical Centre) had a free-swinging gondola, allowing a Gx-load of 3g since the subjects were in a supine position. The results show a statistically significant decrease in OT of 10% after the centrifuge run compared with the baseline measurement. This implies a reduced gain of the otolith system as a consequence of prolonged exposure to an increased G-load. Although spatial orientation involves more systems than the otolith system alone, the vestibular adaptation found here implies that a subject should underestimate the angle of body tilt after a centrifuge run relative to the baseline measurement before the centrifuge run. Preliminary data of the perceived tilt angle, reported verbally by the subjects, support this assumption.

◆ **How does locus of attention change before and after learning Kanji characters?**

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Traditionally, Kanji (Chinese characters) is taught by first teaching the stroke order and then teaching the structure of the Kanji to explain the meaning. However, it is now considered more effective to teach the Kanji structure together with the stroke order, particularly when it is taught to a learner whose mother language is based on the alphabets. Therefore, we investigated the locus of attention while subjects viewed a Kanji and the learning rates by means of two different instruction techniques, namely, 'structure with stroke order (SS)' and 'stroke order alone (S)'. In the lessons, Kanji shape was taught but not the meaning. Twelve subjects, six in each condition, were beginners, and studied eight Kanji characters in a forty-minute lesson.

After the lesson, we measured the eye movements to examine the locus of attention and the effectiveness of each teaching technique with reproduction tests. Test stimuli for measuring eye movements were displayed on an HDTV screen with a viewing angle of 20 deg. The results were as follows. (a) After the SS instruction, fixations were concentrated on small areas of the screen. The locus of attention was similar to that of intermediate-level learners that we found in another experiment. However, after the S instruction, fixations were scattered over a larger area on the screen. (b) After SS instruction, fixations were concentrated on the parts that potentially carry information, even for a complicated unknown Kanji character. (c) Reproduction rates were same in two conditions, but, after the SS instruction, some errors in the reproduction tests consisted of substituting meaningful parts. The results (b) and (c) suggest that subjects learn Kanji characters by learning subparts when they have structural information. Thus, we conclude that the SS instruction is suitable for beginners.

◆ **Modeling the formation of image-viewing trajectories**

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A model for studying image features in the peripheral visual field that excite a switch of the fixation point of the eye has been developed. The structure of the 'attention window' in our model allows parallel information processing in the central (foveal) region and in forty-eight peripheral regions (on the intersections of sixteen radiating lines and three concentric circles) for each fixation point. The model was tested in computer simulations for image processing of human faces. As an initial fixation point we chose the raster center or any point indicated by the operator. A possible central region for each next fixation point was chosen from among the peripheral regions of the previous fixation point, depending upon the following image-fragment parameters: intensity, value of contrast, size and number of oriented elements, differences in orientations of central and peripheral elements, and distances from previous fixation points. The contribution of different parameters of image features that provided the most similarity between viewing trajectory formed by the model algorithms and that formed by the operator was tested. The results of computer simulations allow us to make a set of predictions on possible properties of a biological prototype: (i) the existence of discrete centers of visual-information processing in the retinocortical system that may be areas of attraction when the fixation point is chosen; (ii) the existence of a critical (for a switch of view) value of differences between the orientations of linear segments located in the foveal and peripheral fields of vision; and (iii) angles and intersections of oriented elements as features exciting the shift of view.

◆ **How to control a low-vision aid**

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Perception cannot be studied without reference to movements. This is also the case for 'pure' perceptual tasks like reading. For people with low vision (LVP), movement control is still more important. They have to synchronise the eye movements with the movements of the magnifier. LVP do not have typical saccadic movements, but move their eyes according to a sawtooth pattern. While moving the magnifier smoothly along the line, they keep their eyes on the same location in the image. As soon as the recognition process is completed, the eye jumps to the next fixation point in the image (optokinetic nystagmus). Recently some research has been done on factors that determine the relatively slow reading rate of LVP using this technique. In this research another important aspect of reading, the search process, has been neglected. It is shown that in most designs of low-vision aids (LVA), little or no attention is given to this essential part of the reading process. As a consequence, during searching, bigger losses in reading speed are to be expected (and were found in our research). In other words, bigger losses in reading speed are found when tasks that are more ecologically valid are used to evaluate reading performance of LVP. Suggestions are given on how to improve the design of LVAs to enable LVP to profit from their residual vision to support the search process in reading. Finally, a similarity is demonstrated between manipulation of LVAs and 'manipulating with' and 'navigation in' large communication systems (Dillon, 1992 *Ergonomics* 35 1297-1326).

SPATIAL VISION

◆ **Size discrimination in different visual fields: magnitude of 'equal-images' illusion in the fovea**

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In a previous study a difference in thresholds was found for size discrimination of two-dimensional contour images in the upper and lower visual fields (Chukova, 1992 *Perception* 21 Supplement 2, 100). For the left and right visual fields, no significant difference has been found, though physically identical images are perceived as different to the left and right of the fixation (Chukova and Gusev, 1993 *Perception* 22 Supplement, 121). In this study, the values of size underestimation or overestimation in different visual hemifields were calculated from the psychometric functions at the correct-responses level of 50% (when the reference and the test stimulus were estimated by the observer as being equal). Four subjects monocularly performed the size-discrimination task with black-contour squares (the reference) of twenty-seven sizes ranging from 8 to 60 min, in increments of 2 min, and five test rectangles (with height decrements of 1.25%). The observer had to decide whether the rectangle was above or below, and to the left or to the right of the square.

It was found that the threshold difference is conditioned by the size overestimation in the upper visual field by about 2%–3%; in our study these values exceed the difference between the first (or even second) of the five test stimuli and the reference, so that when the test stimuli are presented above the reference, they are overestimated enough for the thresholds to be increased (and decreased when presented from below, owing to the overestimation of the reference). Expressive vertical asymmetry in the central visual field of 2.5 deg is observed for most of the sizes used. Clear horizontal asymmetry in the fovea has not been found. Images presented along the horizontal axis are overestimated by the same values (2%–3%), both to the left and to the right of the fixation point.

◆ **Length representation in each hemisphere**

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When normal right-handed subjects have to mark the middle of a line, they make a small but significant leftward deviation of the subjective middle. It was suggested that this leftward bias was related to an overactivation of the right hemisphere in response to the spatial nature of the task. Such an overactivation of the right hemisphere might result in an enhancement of the left perceptual hemisphere, which would lead in turn to a leftward deviation of the bisection (Bradshaw et al, 1987 *Neuropsychologia* 25 735–738). To test the hypothesis of an 'enhancement' of the hemisphere contralateral to the most activated hemisphere, forty-five normal right-handed subjects performed an adaptation of the line-bisection protocol. The subject was given a half-line (left half, protocol P1; or right half, protocol P2), and had to complete it in order to obtain a whole line with two equal halves. The conjunction of the spatial nature of the task and of the presentation of the left half of the line in protocol P1 is expected to activate the right hemisphere which in turn would lead to an enhancement of the left-half representation and to an overconstruction of the right half. On the contrary in protocol P2, the reverse bias is expected, ie overconstruction of the left half. Results show no significant bias when the subject had to infer the right half from the left one, whereas building the left half from the right one led to a significant underconstruction. The enhancement and hemispheric-activation hypotheses [Kinsbourne, 1973, in *Attention and Performance* volume IV (New York: Academic Press) pp 239–255], are discussed, but do not appear compatible with our results. Rather, it is suggested that there is a preferential direction for construction, possibly related to reading habits.

◆ **A hysteresis model for the temporal dynamics in the Ehrenstein illusion**

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Ehrenstein figures of various aspect ratios and with central apertures of 0.5, 1.0, and 2.0 deg in diameter were used to study some quantitative properties of aspect change. In the experiment, the bar width of the Ehrenstein figures was manipulated randomly or serially (in ascending and descending order), while the subjects had to judge whether they saw a square or a circle.

Plotting the relative frequencies of the judgments against bar width, we obtained nonlinear switching functions of sigmoidal shape, which showed a constant ratio of the switching threshold (the critical bar width corresponding to 0.5 probability of judgment in favour of bar or circle) to the diameter of the central aperture, and an increase in slope with increasing diameter of the central aperture. The sigmoidal switching functions obtained for ascending and descending manipulations of bar width were shifted in parallel on the bar-width scale, meaning that the aspect change evoked by the changing width shows hysteresis. Since the area closed by both functions represents the work required to take the system through the whole memorisation cycle, we used it as a measure of the amount of memorial energy. Letting the subjects repeat the memorisation cycle many times and computing the area of the hysteresis loop, we obtained time series of memorial energy with stationary and nonstationary behaviour in different time intervals. The behaviour of the time series can be modelled with a nonlinear dynamic system consisting of a large number of binary neurons.

◆ **Limits of illusory-contour integration in the Ehrenstein illusion**

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We wanted to determine the spatial extent over which an illusory contour is perceived in the Ehrenstein figure. Since it is assumed that illusory-contour integration is generated by neurons in V2 (Von der Heydt et al, 1989 *Journal of Neuroscience* 9 1731–1748), the psychophysical limits of such an integration should reflect the mean size of the receptive fields of these cells. In an Ehrenstein figure induced by four lines, we varied the size of the central gap and the length of the inducing lines in order to see at which particular gap size and line length the illusory effect would be cancelled. We presented twenty-five different figures, white inducers on a dark background, on a computer screen. For each figure, subjects had to decide whether they perceived an illusory contour or not by pressing a response key. The gap size varied between 24 and 120 min arc, and the length of the inducing lines between 4.5 and 64.5 min arc. The results show that, at a gap size of 48 min arc and a line length of 19.5 min arc, the subjects perceive the illusory contour on approximately 50% of the presentations. This response level corresponds to the conditions where reaction times are the longest. Generally, the reaction times increase until a maximum, and then decrease. These findings sustain the hypothesis that the perceived limits of illusory contour integration in the Ehrenstein illusion correspond to the mean size of the receptive fields of visual neurons.

◆ **Localisation of singularities in first-order optical-flow fields**

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We investigated the accuracy with which subjects indicate the singular point (the point with zero speed) in a first-order optical-flow field. This accuracy is important in determination of heading direction. Stimuli consisted of moving random-dot patterns showing a divergence, a curl, or a linear combination of the two (spiral motion). The stimulus window was square with sides of 20 deg. We first ran a number of experiments to test the dependence of performance on several parameters. In these experiments, subjects were shown a flow field with its centre at a random location, immediately followed by a grid. Their task was to indicate in which square of the grid the singular point had been located. Performance is independent of presentation period (saturation at 57 ms) as well as of lifetime of the dots. Performance increases with the number of dots, saturating at about 36 dots per frame. For the remaining experiments, we chose to keep presentation period and lifetime of the dots fixed at 228 ms (16 frames) and the number of dots per frame at 64. We found similar results for divergence, curl, and spiral motion. In a second experiment subjects were shown the same stimuli, this time with the singular points at one of fifty locations. Subjects indicated the exact point at which the singular point had been situated (no grid was presented). In this way, we obtained a cloud of response coordinates for each of the fifty locations. The shape of these clouds is ellipsoidal with its major axis in the radial direction and its minor axis in the tangential direction. In other words, subjects determine the location of the singularity more accurately in the tangential than in the radial direction.

◆ **Spatial integration for polar-circular gratings with various frequency gradients**

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We have recently modelled the human foveal visual system in a detection task as a simple image processor comprising (i) low-pass filtering due to the optical modulation transfer function of the eye, (ii) high-pass filtering due to the neural modulation transfer function of visual pathways,

(iii) addition of internal neural noise, and (iv) detection by a local matched filter, whose efficiency decreases with increasing grating area. According to the model, contrast sensitivity with grating area is described by $S_{rms} = S_{max}(1 + A_c/A)^{-0.5}$, where S_{rms} is rms contrast sensitivity, A is grating area, S_{max} is maximum contrast sensitivity obtainable by spatial integration, and A_c is critical area marking the saturation of spatial integration. We have now tested applicability of the model by measuring binocular rms contrast sensitivities and contrast-energy thresholds for polar-circular cosine gratings with various spatial-frequency gradients. The local spatial frequency decreased with the increasing distance from the image centre. The cosine gratings were calculated as $L = L_0\{1 + m\cos[2\pi f_c \ln(gr + 1)/g]\}$, where L_0 is average luminance, m is Michelson contrast, f_c is central spatial frequency, g is gradient, and r is grating radius. In agreement with the model, contrast sensitivity first increased at small grating areas (A) in direct proportion to the square root of area but when grating area exceeded its critical value the increase saturated and contrast sensitivity then became independent of area. The critical area and maximum contrast sensitivity of spatial integration were first constant but then decreased with increasing gradient. The explained variances were typically 97%–99%, irrespective of frequency gradient. By transforming the rms contrast sensitivities to contrast energy thresholds (E_{th}), the increase of threshold with grating area could be described by $E_{th} = E_0(1 + A/A_c)$, where E_0 is the energy threshold at grating areas much smaller than A_c . E_0 was found to be independent of frequency gradient.

- ◆ **Dimensions and characteristics of contour interaction in monocular and binocular vision**
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In many clinical tests different images are used for the two eyes. Two effects have to be considered, binocular rivalry and contour interaction (Kaufman, 1963 *Vision Research* 3 401). The aim in this work is to investigate the width and the localisation of the contour-interaction region, the difference between monocular and binocular vision, and the influence of contrast on the other parameters. For this purpose a psychophysical test is used. An incomplete cross with the centre part blanked is presented. Each subject is asked whether a central 'X' is seen and the localisation (central, up, down, left, right) of this pattern when it is seen. Reducing the size of the central blanked region until the 'X' pattern disappears allows us to measure the maximum width of the interaction region. It is also possible to study the influence of some factors on the characteristics of the interaction region by changing the contrast level in monocular and binocular vision. The results of this work showed that the edge of this region has a sigmoid shape with a discrimination threshold depending on the contrast level.

- ◆ **Learning in blur discrimination of moving edges**
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Blur-discrimination thresholds for moving, Gaussian-blurred edges were measured to separate the effects of motion blur and static spatial blur. The data were modelled by assuming a linear transform of the physical image of the edge to its neural representation. The model consisted of three components: a static spatial filter, a velocity-dependent spatial filter, and a comparison mechanism (Weber fraction). The model fitted well to the data of each of the three observers used in this part of the study. When one of the observers repeated the experiment six months later, after many other experiments mainly with small reference blurs, changes in thresholds and model parameters were found. Thresholds for small reference blurs were lower but, for example, thresholds for a reference blur of 4 min arc were, on average, about 0.15 min arc higher in this experiment than they were in the original experiment. Thus, it seems that the visual system is paying a price for the improved performance at small reference blurs: the performance at higher blurs declines. In the modelling, the best-fit estimate for the space constant of the effective static spatial filter showed a decrease from almost 2 min arc to about 1 min arc. The results indicate low-level learning and neural plasticity in the blur-discrimination system. A surprising result came from an experiment in which the contrast polarity in relation to the direction of motion was changed to be opposite to that in the original experiment. The learning effects for moving edges were not transferred from one polarity to the other. Thus, spatial analysis of moving objects may be served by two separate subsystems, possibly related to the on and off systems of the visual pathway.

BRIGHTNESS AND LIGHTNESS

◆ An observation of lightness constancy by three-dimensional movement of an object on a CRT display

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Gilchrist's work (1979 *Scientific American* **240** 88-97) has centered on the conditions under which the visual system can distinguish reflectance edges from illumination edges and on how the distinction might be made. He was guided by the belief that the classification of edges cannot be carried out at the level of the retina. This means that not only the eye but also the central nervous system plays a role (depending on depth information) in the classification of edges. Schirillo et al (1990 *Perception & Psychophysics* **48** 82-90) have simulated the Gilchrist situation on a CRT display, by means of stereopsis, and have obtained results for lightness that follow the same pattern as those of Gilchrist. When a trapezium is gradually transformed stroboscopically on a CRT (ie $\square \rightarrow \square \rightarrow \square$ in sixteen steps), the observer cannot perceive a two-dimensional change of form, but perceived a three-dimensional rotation of an invariant rectangle. When I changed the lightness of the gray surface of this quadrilateral synchronously (ie white \rightarrow gray \rightarrow black), the observer could not perceive the change of the brightness of the illuminant, but perceived a change in the impression of a shadow on the constant gray surface. By means of this experimental situation, by the method of estimation, I could confirm the lightness-constancy effect with a CRT simulation.

◆ A dynamical model for retinal brightness processing

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Psychophysical evidence has shown that brightness adaptation involves both subtractive and divisive gain-control processes. The purpose in the present research is to incorporate these two processes into a quantitative model for brightness adaptation that is based on known retinal circuitry. The resulting model consists of coupled, nonlinear differential equations describing responses of the various types of retinal neurons. As retinal anatomy indicates the presence of several feedback paths, both subtractive and divisive adaptation processes were modeled as feedback circuits. The model incorporates circuitry both for on-center and for off-center varieties of M and P ganglion cells. In the model the physiological differences between M and P cells result from their different receptive-field sizes and from a slower temporal response in the midget (P) bipolar cell. The resulting model accounts for a wide range of brightness-adaptation phenomena including changes in the shape of spatial and temporal contrast-sensitivity functions as a function of mean luminance and afterimage formation. In conclusion, a nonlinear dynamical model incorporating feedback-gain controls is consistent with retinal anatomy and physiology and can explain a wide range of psychophysical phenomena related to brightness adaptation.

◆ Modelling spatial brightness by syntactical summation

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Models of brightness perception usually consist of different bandpass filters called channels whose responses are (non)linearly processed and combined. In such low-level models the fact is ignored that brightness involves higher-level effects related to a pattern interpretation, eg the Koffka-Benussi ring. A new approach is to compute a syntactical or symbolic image representation in terms of multiscale lines and edges, and to combine this symbolic information in the construction of a brightness map. Our model consists of roughly the same components as that described by Kingdom and Moulden (1992 *Vision Research* **32** 1565-1582), but includes (a) a multiscale line and edge detection on the basis of Gabor functions, (b) a scale-stability analysis which suppresses unreliable information due to response-interference effects, and (c) low-pass filters that govern the generation of global and local background levels. The brightness map is obtained by summing all information, where lines are represented by Gaussian functions and edges by Gaussian-enveloped error functions. Although the model under study is far from being optimised with respect to exact psychophysical data, it can predict a variety of one-dimensional effects, including the two opposite forms of brightness induction (assimilation and simultaneous brightness contrast), Mach bands in trapezoid gratings, as well as the Chevreul and Craik-O'Brien-Cornsweet illusions.

◆ **Nulling of brightness fading in a Ganzfeld**

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We investigated sustained brightness perception and brightness fading in a Ganzfeld. Our aim was to quantify the time course and magnitude of fading as a function of adaptation level. Subjects were exposed to constant luminance levels, ranging from 0.1 to 10 cd m⁻², while looking into a uniformly illuminated sphere. In order to quantify subjective brightness, we employed two measures—a magnitude-estimation method in which the subjects' task was to specify the progressive decrease of perceived brightness due to fading, and a nulling method in which the subjects were instructed to keep the perceived brightness constant by adjusting the luminance.

For a given luminance value, perceived brightness decreases after a brief period approximately in a linear fashion and levels off after 5–15 min. The final level depends on the adapting luminance as well as on the attention of the observer and is often accompanied by sensations of a bluish colour. Only in some cases does the final plateau approach the subjective Eigengrau. 'Nulling' requires an approximately linear increase of luminance, over a similar period of time as found for magnitude estimation. Total increment size (added luminance) and slope of the nulling curve are proportional to adapting luminance (ie vary by the same factor). Under Ganzfeld illumination, sustained brightness perception is severely impaired. After prolonged exposure, the steady-state percept is that of an intermediate grey somewhat above the Eigengrau. The finding of a constant proportionality factor for total increments and slopes suggests that brightness fading depends on a multiplicative process, with a slow time constant.

HIGH-LEVEL VISION

◆ **Illumination dependency in object recognition**

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How can objects be recognized, given that images differ drastically in a way depending on the illumination? The standard answer is that, early on, the visual system extracts illumination-invariant features, such as edges and contours, but discounts spurious features, such as shadows and specularities. However, exemplar-based theories propose that object representations may be tied to the original image (particularly given that illumination features are difficult to discount by using low-level mechanisms). This leaves open the issue of whether recognition is sensitive to the illumination conditions under which an object is learned. This was investigated by using objects synthesized by compositing simple three-dimensional volumes and illuminated with ambient and point light sources from either the left or the right, and varying both the shading and the shadows cast on the objects. In experiment 1 we employed six objects; images of objects were briefly presented, followed by a mask (a random composition of simple three-dimensional volumes illuminated from both directions), and then a second object, also masked. The crucial manipulation was whether there was a change in illumination across the two objects. Observers judged whether the objects were the same or different regardless of illumination. A significant performance cost across illumination changes was found for correct 'same' responses, but not for 'different' responses. These findings are consistent with illumination-specific representations in that illumination changes may affect performance only when there is a match between perceived and remembered objects. In experiment 2 we employed an identical paradigm with six object pairs sharing parts. Such subtle shape discriminations produce strong view-point dependency in recognition—here we tested whether such contrasts would prompt stronger illumination dependency. Results were similar to those of experiment 1: a performance cost across illumination change for 'same' responses, but no cost for 'different' responses. However, this effect was only slightly larger than that found previously. These results indicate that object representations in recognition are specific to illumination-dependent image features and support exemplar-based theories in which representations preserve many features of the original image.

◆ **Evaluating view-dependent and view-independent theories of object recognition by multiple regression analyses of psychophysical data**

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By means of computer graphics, twenty-five familiar objects were constructed from so-called geons (geometric ions) and twenty-five different views for each object were prepared by rotation

around the x -axis (roll), the y -axis (spin), and the z -axis (turn). A total of 625 stimuli were presented on a display and the subjects were asked to name the stimulus as fast as possible and to rate its canonicity. Multiple regression analyses revealed that the canonical ratings and the percentage of correct responses were well explained by the visible geon numbers and their visible principal-axis lengths. However, for the reaction times, these two variables showed no significant regression coefficients. Instead, the degree of rotation from the most-canonical views, especially around the z -axis and the x -axis, strongly influenced the reaction times. These results are discussed in relation to the view-dependent and the view-independent theories of object recognition. The psychophysical data obtained suggest that human prototypes of objects may be represented as descriptions which have rich information about geon structures, while they have view-independent properties only in small ranges. Therefore, after the prototypes are activated, the verification process by rotation is considered to be necessary to check their correspondence to the observed views. From the results of multiple regression analysis, it can be concluded that the degree of activation of the prototypes affects the percentage of correct responses and that the time taken by the verification process mainly corresponds to reaction times.

◆ **Methods for dense reconstruction in active vision**

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Nowadays, the aims for computer vision are to accomplish ever more-complex tasks, such as controlling a vehicle, avoiding static or moving obstacles, or three-dimensional (3-D) matching for supervision. A precise 3-D representation of the environment is needed to achieve these tasks. Our main goal was to obtain a dense 3-D map of the environment from a monocular sequence of images acquired by an active vision system (robotic head). In order to do that, we explored the various existing methods, comparing their advantages and drawbacks. In the context of active vision, the chosen algorithm was required to be fast. In this work, we assume that the disparity between two successive frames is small, and that the reflectance model is Lambertian. We have combined two 'classical' methods which appear to be complementary—a region segmentation followed by an iterative regularisation. Indeed, a fast convergence of the regularisation process requires a good initial estimate. Moreover, this first estimate should provide a reliable location of depth discontinuities and occlusions for a precise reconstruction of the environment. Therefore, region segmentation seems to be the most adequate. More precisely, a disparity map can be rapidly obtained for regions detected by a fast segmentation algorithm such as the 'toboggan method' where the main parameters are adjusted automatically. The disparity map can then be converted into a good initial proximity estimate for a regularisation process. By noting that occlusions and depth discontinuities are located at the frontiers of regions, one can easily take into account the associated constraints when regularising.

As a conclusion, the combination of two methods does not necessarily increase the complexity of an algorithm. In our case, it provided a fast 3-D dense reconstruction method close to real-time performance and well adapted for the processing of depth discontinuities and occlusions. We validated our approach both on synthetic and on real images.

◆ **Space-perception-in-navigation (SPIN) theory**

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Visual navigation in space is a crucial feature for the survival of the organism. Three theoretical questions were addressed. How are two-dimensional dynamic images transformed monocularly into stable three-dimensional percepts? Is our representation given in veridical or relative terms? How are the perceptual constancy of position and size preserved? A promising solution to these problems may reside in the analysis of the optic flow. This is called 'passive navigation' as compared with 'active navigation' where extraretinal signals are utilised. However, earlier analyses of the optic flow (Simpson, 1993 *Spatial Vision* 7 35–75) led to a solution up to a scalar in the velocity vector, creating the indeterminate-scale problem and providing relative depth only.

The space-perception-in-navigation (SPIN) theory provides a unique solution both to passive and to active navigation. The solution for the passive-navigation problem has shown that all the information required to reconstruct the three-dimensional world in metric terms exists in the optic flow, as suggested in Gibson's direct-perception theory. Earlier work solved the navigation problem for pure rotations (Hadani et al, 1994 *Journal of the Optical Society of America A* 11 1564–1574). The radius of the eyeball was the metric unit. We have shown how the flow equations are solved for six degrees of freedom (Hadani and Kononov, 1994 *Journal of the*

Optical Society of America A, in press) for two views and three rigid points. A differential solution was obtained for a single point, which eliminates the need for rigidity assumption. Solving for passive navigation enables the system to project the points out in space into their veridical positions. Thus it provides a representation in object-centered coordinates, and preserves the constancies of position size and shape. The derivation of both the discrete and the differential solutions is based on Euler's theorem for rigid movement. The solution for a single point was possible by distinguishing between a mathematical point, and a visual point. In this work we present current developments of the SPIN theory demonstrated by a computer simulation.

- ◆ **Grasp points on virtual three-dimensional objects: independence from visual contour**
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In this study we compared human grasp performance with real and virtual objects in a precision-grip task. The theoretical optimal grasp points on a visual shape can be calculated according to the theory of planar grasp. The optimal grasp points are obtained from the mutual intersection of the local symmetry and antisymmetry sets, and the critical set of the configuration space of all possible grasp points. To compare human grasp performance between real and virtual objects, 120 grasp trials with flat plastic tiles were recorded with a movement-tracking system (Optotrak, Northern Digital). A reaction time of 520 ± 130 ms between stimulus display and final grasp position of middle and forefinger suggest that the objects were not scrutinised before grasping. The same number of grasp trials were repeated with virtual objects displayed on a computer monitor to produce realistic stereoscopic images 15 cm in front of the screen. The grasp points were the same, with a standard deviation of $\pm 7^\circ$, showing that missing tactile feedback is not degrading grasp performance. In order to test which representation (two-dimensional versus three-dimensional) the planning of grasp movements is based on, the following two experiments were performed. (1) The planar shape rotated at 8° s^{-1} around the viewing direction. The deformation of the contour was therefore only a rigid rotation in the image plane. (2) The planar shape was rotated around a horizontal axis and the projected image deformed nonrigidly. During the prehension movement the hand followed the stable grasp point up to $\pm 40^\circ$ of that particular object. In case (1) the results were consistent with the theory because of the whole view of the shape. The average reaction time was 570 ± 160 ms. If the object is rotated in depth at an angular speed of 8° s^{-1} , the deformation of the visible contour does not lead to a new set of grasp points, thus suggesting that a three-dimensional representation of the object is used for grasp planning. The reaction time of 620 ± 180 ms suggests a more-complex processing for task planning.

- ◆ **Effects of moving textured backgrounds on visuo-oculo-manual tracking in humans**
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In order to determine which visual information is used to control complex movements, we investigated how a moving background changed both the eye smooth pursuit and the open-loop manual tracking of a small target that suddenly started to move rightward at a constant velocity (12.5 deg s^{-1}). Backgrounds consisted of randomly distributed small white dots, projected on a video display. They moved either leftward or rightward, with two velocities (14 and 6 deg s^{-1}). Moving-background conditions were interleaved with a static-background condition. Subjects were instructed to track the target as soon as it started (-10 deg) and to stop the tracking when the target disappeared ($+10 \text{ deg}$). Eye movements were recorded with an infrared limbus detector and forearm rotation was recorded with a linear potentiometer fixed in with the elbow-rotation axis of a manipulandum.

When the background moved against the target, the smooth-pursuit velocity gain of the eye was significantly lowered. Conversely, when its background moved in the same direction as that of the target, velocity gain was increased. Initial and steady-state eye velocities were found to be linearly inversely related to the background velocity. Subjects compensated for these changes in pursuit velocity by an increase in catch-up saccades, such that the displacement gain remained close to unity. Inverse modulations were observed for manual tracking. When the background moved leftward, initial and steady-state manual-tracking velocities were accelerated, whereas they were lowered when the background moved rightward. Changes in manual-tracking velocity were linearly related to background velocity, as well as to the retinal slip of the target. These results are consistent with motion perception observed in such conditions. We suggest

that the manual motor system uses perceived, and not real, target velocity, which is constructed by summation of a retinal velocity signal and an efference-copy signal arising from the ocular-pursuit generator.

◆ **How do variations in speed of optical flow affect locomotor control?**

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Optical flow has been shown to play an important role in the regulation of speed of locomotion but decisive questions concerning its perception remain as yet unanswered. How is locomotor regulation implemented? Is control of locomotor speed determined once and for all at the onset of the locomotor trajectory or is there a continuous updating of walking speed according to optical environment conditions? Also, do we make the same use of this optical information at different stages of our lives? In order to understand better such processes and their evolution with age, children and adults were studied while walking in a moving texture (approaching or receding) of luminous dots projected onto the ground surface; at the middle of the course the texture movement was suddenly accelerated or decelerated. Locomotor speed was recorded and compared before and after the modification in texture speed for eleven adults and thirty-two children (8, 10, and 12 years old). Results show that, although adults tend to walk slower in an approaching texture than in a receding or fixed texture, they seem unaffected by an acceleration or deceleration for both directions. Children also slow down in an approaching texture, but, in contrast to adults, they further reduce their walking speed when texture movement accelerates. They also slow down after an acceleration of a receding texture. The younger children were the most affected. Thus it would seem that children and adults do not treat optical-flow information in quite the same manner. While the latter appear to maintain a predetermined locomotor speed independently of on-line variations in optical flow, the former seem essentially sensitive to the acceleration component of the optical flow, as they slow down in both directions of acceleration. Children's reactions in walking speed seem more determined by optical environmental conditions than adults.

◆ **Estimating distance to an 'ever-fleeing' target**

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The aim in this study was to determine to what extent distance estimation is influenced by local visual cues surrounding a target. A computer-generated dot texture was projected onto a vertical screen situated at the far end of a large room. Spacing between the projected dots was defined so as to vary automatically with subjects' displacements. A luminous diode (target) was placed on the screen at eye height and at the centre of the projected texture. Twenty-four adults had to walk and to stop one metre in front of the target. In a first, control, condition (CC), texture-dot spacing remained unchanged (retinal expansion only due to the subject's approach). In a second condition (CA), the visual angle to the dot texture was kept constant independently of the subject's distance to the target. In a third condition (DT), texture size decreased with the subject's approach, inducing a relative retinal contraction (accelerated fleeing target). For the fourth condition (IT), texture expansion was increased and also subserved to locomotion (texture expands at a rate greater than that of a normal approach). We expected that for condition CA subjects would perceive the target as 'ever fleeing' or moving away from them at the same speed as their locomotion. For condition DT subjects would perceive the target as moving away from them at a speed superior to their locomotor speed, the opposite effect being expected for IT. Results show that subjects stop closer to their starting point in condition IT, showing an underestimation of target position as compared with in the control condition (CC). For conditions CA and DT they tend to stop much closer to the target than in the control condition. These results show that angular change in optical information locally attached to a target is necessary to control distance estimation in walking.

◆ **Face perception at various eccentricities**

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Since visual performance in many other tasks can be made equal across the visual field simply by an appropriate change of scale, we investigated whether this would also be the case with face discrimination, a spatially complex task. We utilised a method by which a desired amount of geometrical distortion is introduced into an image of a face. First, a discrete Fourier transform was performed on the original face image and the transformed image was bandpass filtered with a circularly symmetric log-Gaussian transfer function. Then the inverse Fourier transforms were used to produce the distortion matrix and the image was distorted by using this matrix.

The values in the matrix indicate the amount by which the image will be increased or decreased at each location in the image. The amount of distortion can be adjusted in infinitely small steps by amplifying/attenuating the magnification matrix. Threshold distortion was expressed in terms of correlation sensitivity $S = (1-r)^{-1}$, where r is the correlation coefficient between the undistorted image and the least-distorted image that allows discrimination from the undistorted image. Sensitivity was determined by using a two-alternative forced-choice method at several eccentricities for a series of face stimuli, all of which simply were magnified or minified versions of one another. Eccentricity dependence was thus determined by using the method of spatial scaling. It requires no assumptions regarding the size of visual stimuli to be presented at various eccentricities. E_2 refers to the eccentricity at which foveal stimulus size must double in order to maintain performance equivalent to that at the fovea. It was possible to equate foveal and peripheral performance, and E_2 of about 2 deg was found for this task. The eccentricity dependence corresponds roughly to the decline in orientation and curvature discrimination determined previously with the method of spatial scaling.

◆ **Visual object recognition: interaction of axis foreshortening and object type**

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Humphreys and Riddoch (1984 *Quarterly Journal of Experimental Psychology* **36** 385-415) demonstrated, in five brain-damaged subjects, that viewpoint changes can affect object recognition in two ways: through foreshortening of the elongated or principal axis, or through occlusion of relevant features. Whereas they manipulated viewpoint in an all-or-nothing manner, we have studied the relationship between viewpoint and recognisability systematically and in sixty normal subjects. Ninety-six line drawings, depicting sixteen objects from six different views, were presented tachistoscopically, starting below recognition threshold. The exposure time required for recognition was determined by systematically increasing exposure time over repeated presentations of a drawing. Half of the objects were 'flat' (impossible to recognise in front view, eg scissors), the other half 'fronted' (recognisable in front view, eg shoe). Viewpoint manipulation started from the left side view and consisted of a counterclockwise in depth rotation (six steps) around the vertical axis, ending at 80° in flat and 90° in fronted objects. For half of the objects this manipulation resulted in a foreshortening of the principal axis, for the other half in a foreshortening of a nonprincipal axis. Our results indicate that the effect of viewpoint becomes apparent only at higher levels of depth rotation. Up to 54°, exposure time for recognition is centred around 85 ms. Thereafter it increases progressively, the endpoint depending on object type: 620 ms for flat (80°) and 420 ms for fronted objects (90°). Surprisingly, the same relationship is obtained by foreshortening of the primary and a nonprimary axis. This last finding may suggest that it is not the amount of information contained in the foreshortened side, but the amount of distortion of whatever information is there, that determines the impact of the manipulation.

◆ **Visual object recognition: unconventional object views and high-resolution information**

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A drawing of an object needs to be perceived for a certain length of time, before it can be identified. This exposure time for recognition progressively increases with foreshortening of one of the axes of the object. Since it is plausible that foreshortening causes a distortion of the global shape of the object form, making recognition dependent upon details in the drawing, a possible explanation for this might be that high-resolution information needs more time to be processed. If this is the case, recognition thresholds for less-foreshortened object views should be more resistant to optic blur than thresholds for highly foreshortened views.

To test this hypothesis, exposure time for recognition and resistance to optic blur were compared for twenty drawings representing ten objects, each with a low and a high degree of foreshortening. All drawings were sized to fit a circle encompassing 6 deg of visual angle, to compensate for the surface reduction due to rotation in depth. Resistance to blur and exposure time for recognition were determined in an analogous manner: for exposure time, by tachistoscopically controlling duration of exposition; for resistance to blur, by binocular optical defocusing. In either case recognition threshold is determined by starting at a visual constraint level below threshold, and systematically decreasing the constraint. An inverse relationship was found between exposure time to recognition and resistance to optic blur: less-foreshortened object views required smaller exposure times and exhibited a higher resistance to blur (79 ms

and +4.7 diopters, respectively) compared with highly foreshortened views (237 ms and +2.8 diopters, respectively). The Spearman rank-order correlation between exposure time and resistance to blur was -0.595 . This strongly suggests that the recognition of objects under highly foreshortening conditions depends on high-resolution information.

◆ **The subjective vertical as a function of directional information in the visual field**

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Whenever the head is tilted sideways, the retinal image is necessarily subjected to counter-rotation. The fact that this counter-rotation has no effect on perception is thought to be due to a compensatory process [see, for example, Bishop, 1974, in *Handbook of Sensory Physiology* Volume 6, Part 2 *Vestibular System* Ed. H H Kornhuber (Heidelberg: Springer) pp 155–190]. Such a compensation is mediated by the interaction of visual and otolith signals. We measured the influence of a visual background pattern on the adjustment of the subjective vertical. The entire background pattern was made rotatable in the fronto-parallel plane around the subjects' visual axis. The subjects were fastened in a centrifuge apparatus, which allowed the recording of their adjustments for different body tilts. The experimental parameters were (1) background patterns with a varying amount of directional cues (visual-induction component) and (2) the variation of lateral body tilt (otolith component). (3) We extended this procedure by also recording the adjustments under increased gravitational conditions (1.5g, 2g). (4) During the experiments we also measured the ocular counter-rotation, ie the movement of the eye around its visual axis.

The slow orientational changes of the visual background produced adjustments oscillating around the setting of the subjective vertical without visual induction. It turned out that the mean amplitude of the visual influence also depends on a gravity-based component. Among the organs of the otolith system, this component could be accounted for by the afferent signals of the utricles, which are also considered to control the ocular counter-rotation. On the basis of the results, different concepts for understanding visual and otolith interaction in static orientation are discussed with regard to the information processing structure of the subjective vertical.

◆ **Perceptual, decisional, and attentional components in the speeded verification of object presence in real-world scenes**

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Tachistoscopic research on the visual perception of complex scenes has suggested that context-congruent object processing in realistic environments is massively parallel and virtually unaffected by acuity limitations (Biederman et al, 1982 *Cognitive Psychology* **14** 143; Boyce et al, 1989 *Journal of Experimental Psychology: Human Perception and Performance* **15** 556). However, an analysis of the speeded-target-verification paradigm underlying this claim indicates three possible courses of unreliability in the employed measures of object perceptibility: (1) confounding of perceptual and decisional processes, (2) confounding of direct and attentionally mediated effects on object processing, and (3) confounding of object-feature analysis and object-feature detection. Three experiments are presented in which we attempt to unravel the relative contribution of these components to speeded-target-verification performance. The results indicate that speed and accuracy of object verification are strongly influenced by decisional processes; the presence of briefly flashed, extrafoveally located objects is inferred rather than perceived. There also is a smaller perceptual advantage for context-congruent objects, which, however, appears to be sensitive to deliberate attentional strategies used by the subjects. These findings are discussed in terms of their implications for the development of an adequate paradigm to study the role of real-world knowledge in the perception of real-world scenes.

◆ **Characteristics of competitive networks trained on natural images**

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Previous work by Barrow (1987 *Proceedings of IEEE 1st International Conference on Neural Networks* IEEE number 87TH0191-7) has shown that when unsupervised neural networks are presented with signals that approximate the outputs from lateral geniculate units they develop receptive-field profiles that resemble those of simple cells. Such a learning process might therefore provide a plausible mechanism for the development of cortical receptive fields in animals. Barrow's work, however, left a number of questions unanswered. For example, do such networks evolve similar receptive-field formations when trained on different types of

natural image (in other words, is the process robust) and do they produce receptive fields that compare in a quantitative fashion with typical simple-cell receptive fields?

We have investigated how different parameters affect the organisation of the receptive fields that arise during the training of competitive-learning networks. These parameters included, among others, the effect of using different natural images for training, different variants of the competitive-learning algorithm, and different windowing strategies. The responses of the units in the trained network were quantified in terms of their spatial-frequency and orientation-tuning characteristics. The results show that, like simple cells, the units that evolve are selective for both frequency and orientation, but the characteristics of the receptive fields differ somewhat from those of simple cells.

◆ **The role of central and peripheral image cues in scene recognition**

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Few researchers of perception of real-world scenes will challenge the claim that thematic identification of everyday environments can be achieved within 150 ms. However, there is considerably less consensus on which image cues are instrumental for rapid scene recognition. In the present study we concentrate on the relative importance of centrally and peripherally located information in this recognition process. Speed and accuracy of scene interpretation are measured under tachistoscopic viewing conditions in a direct-identification task and in a semantic-judgment task. Stimuli are full scenes, partial scenes with only central or peripheral information, and hybrid scenes with conflicting central and peripheral information. Performance is measured as a function of the kind of stimulus, the central or peripheral orientation of attention, and the degree of experience subjects have with the stimuli and the task. The results allow further specification of mandatory and voluntary components in models of scene processing, and are framed in an account of the dynamics of the perceptual span during unrestricted scene exploration (De Graef et al, 1992 *Canadian Journal of Psychology* 46 489).

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